

# **TYLENCHIDA**

**Parasites of Plants and Insects, 2nd Edition**





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# TYLENCHIDA

## Parasites of Plants and Insects, 2nd Edition

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**CABI Publishing is a division of CAB International**

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A catalogue record for this book is available from the British Library, London, UK

**Library of Congress Cataloging-in-Publication Data**

Siddiqi, M. Rafiq, 1934–

Tylenchida : parasites of plants and insects / Mohammad Rafiq Siddiqi.--2nd ed.  
p. cm.

First ed. published in January 1986.

Includes bibliographical references (p. )

ISBN 0-85199-202-1 (alk. paper)

1. Tylenchida--Classification. I. Title

QL391.N4 S49 2000

592'.57--dc21

00-021740

ISBN 0 85199 202 1

Date of publication: November 2000

Typeset in 10/12pt Goudy Old Style by Columns Design Ltd, Reading  
Printed and bound in the UK by Biddles Ltd, Guildford and King's Lynn

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## Foreword

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*'Exegi monumentum aere perennius . . .'* (Horatius)

In the Foreword to the first edition of this book, I wrote: 'Undoubtedly, the representatives of the order Tylenchida are of the greatest importance among the free-living and plant-parasitic nematodes both in science and practice. This is why Dr. Siddiqi's book will be of such significance in the zoological publications of our time and indispensable for everyone working with nematodes. . . . There is no doubt that the present book serves as a milestone in the history of nematology.' This is true for the second edition as well.

On the order Tylenchida, taxonomically and economically so important and, in the Nematoda as a group, so rich in genera and species, two outstanding fundamental works have lately been published. One is *Tylenchida: Parasites of Plants and Insects* by Siddiqi (1986), the other *A Reappraisal of Tylenchina (Nemata)* is by Fortuner, Geraert, Luc, Maggenti and Raski (1987-1988). Both works are of special significance in the history of nematology. However, whereas the latter was composed by the collaboration of an international team of nematologists, the former was truly a one-man work. About this edition of *Tylenchida*, I can say that Dr Mohammad Rafiq Siddiqi, having the widest knowledge and expertise in the taxonomy of this group, has produced one of the grandiose monographs of nematodes for all time.

This second edition of *Tylenchida* is by no means a simple reproduction of the original one, but, although based on it, is essentially a new book. Having accepted several new results of other authors and added the best ideas of his own, Dr Siddiqi has summarized, valued and systematized whatever science could tell us about tylenchid nematodes.

Works that have merited a second edition are very few in our science. The book of Dr Siddiqi is one of those rarities. I was very lucky to have been acquainted with both editions in their manuscript stages, and I am absolutely certain that the *Tylenchida-II* will be as impressive and well-accepted as the *Tylenchida-I* was, or

possibly it will surpass that. It will serve as a 'Bible' for all those who have bound their scientific career to Nematoda, this fascinating group of animals.

The author of the present book, Dr M.R. Siddiqi, has written his name with golden letters in the history book of our science of nematology.

István Andrassy  
Budapest, Hungary  
January 2000



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## Preface

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The first edition of this book was published in January 1986. Since then, a large number of new taxa, from species to family rank, have been proposed in Tylenchida. The usefulness of the first edition can be judged by the fact that almost 1000 copies of *Tylenchida: Parasites of Plants and Insects* that were printed have been sold and that edition is now out of print. Copies used by nematologists have now almost worn out (I am pleased to know from many nematologists that the book was used extensively). Thus the need for the new print/edition of this book has been felt for many years.

Now the second edition is here, thanks to God who gave me the strength and dedication to complete the script, add new data and numerous plates of figures and submit it to CAB *International* for publication. I know that the first edition was very useful for identification purposes and that opinions differed on my system of classification which, by some, was considered inflationary. On my speculative phylogeny, much interest and research were generated. Some accepted my system and enlarged on it while others offered criticisms both constructive and not constructive. Tylenchida is inflationary (many more new tylenchid taxa will be described in the future) as one can see by the enormously large number of new taxa incorporated in the second edition. Furthermore, new data on terminology, morphology, systematics and biology have been added. Some intricate taxonomical problems have been dealt with and (almost) solved and it is hoped that the reader will find this edition extremely useful in identification of taxa in this large group of animals and stimulating for further research.

Among the important changes made in this edition are the upgraded classification, deletion of photographs of pioneer nematologists (due to lack of space in the book), and details of Myenchina, the suborder later raised to an order and which I have now excluded from the Tylenchida. Tylenchida now has four suborders - Tylenchina (with infraorders Tylenchata and Anguinata), Hoplolaimina, Criconematina and Hexatylinina. On the matter of classification, the importance of the methodology used, the phylogenetical discussions and my personal views on

relationships based on working experience on these tiny but not insignificant worms have to be taken into account. I have my own perception of these nematodes and there is every possibility that opinion will differ on the phylogeny and classification of this large group. I have added frequent comments on the diversity, inter-relatedness, biological characteristics and systematics of several genera. I accept the blame if I am called a splitter (recognizing *Bitylenchus*, *Quinisulcius*, *Neodolichorhynchus*, *Telotylenchus*, *Sauertylenchus*, *Paratrophurus*, *Merlinius*, *Geocenamus* as separate genera different from *Tylenchorhynchus* is not splitting but strengthening taxonomy) since my aim in writing this book is to help fellow nematologists as well as all those interested in nematodes to understand the Tylenchida and to have at hand a large amount of information about them. To this end, I have made use of the taxonomic categories of subgenus and subfamily in the classification of several groups. This should help the users of the book who are mostly concerned with the identification rather than the systematics of the genera. Identification and systematics go hand-in-hand, the former is an essential tool for researchers, experimentalists and field workers, while the latter is a toy of mental exercise to play with, for a philosopher or a desk-worker who tries to discover the likely pathways along which species have evolved.

No nematode taxonomic work can be the last word, since our knowledge of these little worms is far from complete. In this field of classification of organisms, systematists have never been in total agreement with each other. The difference of opinion is the way of the progress of taxonomy. When it comes to the placement of taxa in a hierarchic system of classification, the slippery slope of inter-relatedness and establishing evolutionary pathways becomes more difficult to tread. Speculation and personal judgement have to be used in all such matters.

A large number of new tylenchid taxa have been described since the publication of the first edition, and some progress has been made in the study of the morphology, ultrastructure and systematics of the Tylenchida. This has helped greatly in the understanding of the diversity and inter-relationship of various taxa and thus improving upon their classification.

It is my desire that this edition serves its purpose of providing available information on the Tylenchida to laboratory and field workers and as a teaching manual as well as a reference work. The book should be useful in exploring the existing biodiversity in nematodes and in the identification, description and classification of future new genera and species. It is not only a compilation of available information, but the result of my study, analysis and synthesis of Tylenchida as a group on which I have worked for more than 40 years and in which I have the honour of adding a large number of new taxa from suborder to subspecies level (in fact, the largest number of new genera in Secernentea have been proposed by me (see p. 30 and Andr  ssy's (1999): A census of genera and subgenera of free-living nematodes, *J. Nem. Morph. Syst.* 2, 45–68)).

Correct identification is important in working on any other biological aspect of the nematodes. It is particularly so in advisory and regulatory services and in programming control strategies including developing resistant varieties. I have tried to present the scientific names of various species and genera and their synonymies as accurately as possible, but if there remain some errors or omissions, I bear full responsibility for them, and I would appreciate it if these are brought to my notice.

I remember the story of a painter who displayed his beautiful painting in a market place with a foot-note: 'Please mark any mistakes', only to find the next day that the entire painting was blackened by correction marks. Next time, the painter displayed another painting with the caption: 'Please improve upon this painting', and it was left spotless and was appreciated by every passer-by who saw it. So please improve upon my ideas expressed in this book and oblige the scientific community. As regards the recognition and placement of various tylenchid taxa in a system of classification as given in this book, any improvement would be most welcome.

I take this opportunity to thank all those who encouraged and helped me in writing this second edition of *Tylenchida: Parasites of Plants and Insects*, particularly the staff of CABI Bioscience UK Centre (Egham) (formerly International Institute of Parasitology, St Albans). I am grateful to the staff of CABI *Publishing*, particularly Tim Hardwick and Emma Critchley, for editing the manuscript and organizing its publication. I am deeply indebted to Dr I. Andr  ssy for going through the manuscript and making corrections and suggestions for improvement. I offer my appreciation to my wife Rashida for her encouragement and forbearance with my preoccupation with the book since most of the work was done at my home at 24 Brantwood Road, Luton, England, and to my daughter Safia F. Siddiqi of CAB *International*, who has been very helpful, particularly in finding the obscure literature.

Mohammad Rafiq Siddiqi  
Luton, England  
January 2000



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## Preface to the First Edition

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Tylenchida affect human well-being in several ways, principally by inflicting heavy losses on crops and yields of oil, fibre and timber. There is hardly any crop free of these nematodes, which abound in millions in agricultural fields, groves, grasslands and forested areas. It is their large population and not the isolated groups of individuals which harm the plants. They also kill useful and friendly insects, such as aphidiophagous ladybirds and pollinator bumblebees. They can sterilize and kill females of several insect pests of agricultural crops and forest trees, and thus have considerable potential in biological control.

The problems these nematodes pose are enormous, but their importance as a significant limiting factor in agricultural production has only recently received worldwide attention. During the last two decades, the increase in published information on Tylenchida has been exponential, and this has led to problems of assimilation, even for the best equipped nematologists. Although a number of primary core journals are devoted to nematological research, much information remains scattered throughout the less easily accessible peripheral journals so that a comprehensive awareness of the field becomes difficult, especially for workers in the less developed countries. Taxonomic information, being highly specialized in nature, is all the more difficult to obtain.

Tylenchida now comprises 216 valid genera and 2200 valid species (76 genera and 222 species are considered in this book as invalid synonyms and 120 species as inquirendae, dubiae or insertae sedis). New genera and species are constantly being described and taxonomic changes are disquietingly common. In addition, the actual identification of these nematodes is difficult, largely because they are minute (the smallest being only 100  $\mu\text{m}$  in length) and the diagnostic characters are difficult to observe and interpret.

The classification of the Tylenchida has to be inferred from relationships based on morphological, physiological, cytogenetic, embryological and ecological characteristics and character states, since evolutionary change is too slow to be apparent and there are no fossils of Tylenchida to provide evidence of its direction. Inevitably,

personal intuitive judgement and speculation must play a significant part in such a classification.

Since Goodey (1963), the need for an up-to-date text on the taxonomy of the Tylenchida has been greatly felt by students, researchers and professional nematologists alike. The present work is an attempt to fulfil this need. For this purpose, I have given diagnoses of all the valid genera and higher categories of Tylenchida and have listed all the nominal species under their respective genera. I have also tried to give identification keys in a simple dichotomous manner and have emphasized the important diagnostic characters in semi-bold. I have intentionally not given the descriptions of type or representative species of valid genera because it would have made the book unwieldy and probably too expensive. However, I have enlarged the generic diagnoses and have frequently given details of the type-species and etymologies of generic names. Remarks on the biological characteristics and the economic importance of members of family groups are frequently made and, where appropriate, the taxonomy of various genera and families is discussed.

The first three chapters of the book give a general account of the Tylenchida, a historical review, techniques commonly used, analyses of morphological characters, taxonomic methods and the origin, phylogeny, outline classification and characteristics of the Tylenchida. The next four chapters deal with the taxonomy of the suborders Tylenchina, Criconematina, Hexatylinea and Mylenchina, respectively. A comprehensive bibliography of 786 references, including literature cited in the text and references to names of all the genera and higher categories of Tylenchida, has been provided: for references to names of species and subspecies, *Helminthological [Nematological] Abstracts* and the checklist of Tarjan & Hopper (1974) should be consulted. An index of all the taxa in Tylenchida is given at the end of the book. It is my hope that this book should serve as a basic text for students and all field and research workers in plant and insect nematology, plant pathology, plant quarantine and general zoology.

I thank Drs I. Andr  ssy, A. Coomans, D.J. Hunt, E. Geraert, F.G.W. Jones, P.K. Koshy, A.R. Stone and J.F. Southey for critical reading of portions of the manuscript and for their constructive discussions. I gratefully acknowledge the expertise and patience of Barbara Gibson, who, with the help of Beryl Cunningham, Eileen Gordon and Sheila Eames, typed a very difficult manuscript. I am also grateful to the Commonwealth Institute of Parasitology, literature and technical resources of which have provided the basis for my work; to the ex-Director of the Commonwealth Institute of Parasitology, Dr Sheila Willmott, and to the present Director, Dr Ralph Muller, for their encouragement, and particularly to the Assistant Director, Peter Gooch, who organized the publication.

I take this opportunity to thank all my friends and co-nematologists, too many to mention by name, who generously helped me by sending reprints of papers, specimens of nematodes, photographs, permissions to reproduce printed works and especially persons in charge of the nematode collections at the Indian Agricultural Research Institute, New Delhi, the Nematology Departments at the University of California at Davis and Riverside, and the USDA Nematology Laboratory, Beltsville, Maryland, from whom type-specimens were freely available on loan for study.

I am grateful to the UK Natural Environment Research Council for a generous grant towards the cost of some of the illustrations in this book.

Since the major portion of this work was completed at my home in Luton, UK, I would like to put on record my deep sense of gratitude to my wife Rashida for her encouragement, and, perhaps more importantly, her forbearance with my long preoccupation with the preparation of the book, and to my daughters Safia, Salma, Somaiya, Sayeeda and Saboohi and son Soheb, who helped me in various ways including reading the typescript and compiling the references.

Mohammad Rafiq Siddiqi  
St Albans, England  
May 1985





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# I Introduction, Historical Review and Techniques

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## 1. INTRODUCTION

Tylenchida Thorne, 1949 is an Order of nematodes or nemas (Greek *nema*, *nematos* = thread, *eidos* = likeness, resembling) of the Subclass Tylenchia Inglis, 1983 (*nec* Rhabditia Maggenti, 1982), Class Secernentea von Linstow, 1905 (= Phasmidia Chitwood & Chitwood, 1933; Rhabditea Inglis, 1983), Phylum Nematoda Rudolphi, 1808 (= Nematoidea Rudolphi, 1808; Nemathelminthes Gegenbaur, 1859; Aschelminthes Grobben, 1909; Nemata Cobb, 1919).

The terms *nema* (for nematode) and nematology were introduced by Cobb (1932). Chitwood (1957) supported Cobb, arguing that, zoologically speaking, the vernacular word nematode was a corruption of the ordinal name Nematoidea of Rudolphi (1808) which was in use in Germany as the plural equivalent 'Nematoden'. Von Siebold (1848, p. 112) used the ordinal word 'Nematodes' which was modified by Diesing (1861, p. 598) as Order Nematoda. Maggenti (1981, 1982) and Goodey (1963) used the names Nemata and Nematodea for Phylum and Class, respectively, instead of Nematoda, but the word nematode is more commonly used than *nema*. Maggenti *et al.* (1987) stressed that Cobb's (1919) Nemata should be used as a phylum name since Cobb (1919) was the first to exclude all but nematodes from the group. They stated: 'Rudolphi (1808) proposed Leder's "Rundwürms" (gordians and nematodes) as the group "Nematoidea" along with Acanthocephala, Trematoda and Cestoidea in the group Entozoa. Therefore there is no reason to credit Rudolphi for the phylum, as Nematoidea included all "thread-like" forms of roundworms, no taxonomic distinction being made.'

Rudolphi's Nematoidea cannot be rejected on the ground that it included gordians. In fact, the term Nematoden and Nematoda have been continuously in use to-date and gordians had been included within the Nematoda for a very long time. Rudolphi (1808) recognized Nematoidea as different from Acanthocephala, Trematoda and Cestoidea. Gegenbaur (1859) placed Nematoidea, Acanthocephala and Gordiacea in a new phylum Nemathelminthes. Nemathelminthes as a phylum

name has been used as recently as 1951 by Hyman, and Maggenti *et al.* (1987) had accepted that 'Nemathelminthes, still remains since it was the only one clearly defined by Vejdovsky (1866).' The choice of name for the phylum, therefore, is between Nematoda and Nemathelminthes/Aschelminthes and I prefer to use the former because it is more ancient and has been widely used. Hence the phylum name Nemata is rejected. Why should one use the vernacular names nemas or nematas/Nematen when nematodes/Nematoden are available and have been used since the 19th century?

Tylenchida are popularly called tylenchs or tylenchids comparable with aphelelchs or aphelenchids, the latter representing a separate order, Aphelenchida Siddiqi, 1980 (see Fig. 1). The term tylench is now restricted to Tylenchina *sensu* Geraert, 1966 and Tylenchida *sensu* Siddiqi, 1980. The Tylenchida are the largest and economically the most important group of plant-parasitic nematodes. The order also includes a large group, Hexatylinea, which parasitize insect and mite haemocoels. As plant parasites, they have exploited all plant organs including flowers and seeds, but mostly they attack roots (Fig. 2).

Several Tylenchida, particularly the families Pratylenchidae, Meloidogynidae and Heteroderidae, are of great economic importance as parasites of agricultural crops and forest trees. They cause substantial crop losses in many countries, for example in Rajasthan, one of the Indian States, it has been estimated that 60 million rupees (approx. US\$1.5 million) are lost in wheat production due to a single nematode species, *Heterodera avenae*. Sasser's (1979) estimates of crop losses due to *Meloidogyne* spp. in tropical countries show on average losses of 15%. Yield losses in vegetable crops from these nematodes of 50–80% are not uncommon. In South Africa, annual loss of vegetables, cereals and fruit crops of about 14% due to plant-parasitic nematodes (comprising mostly of Tylenchida) has been estimated (Keetch, in Kleynhans *et al.*, 1996).

The plant-parasitic Tylenchida are also called eelworms, phytonematodes, phytohelminths or simply plant nematodes. Their study constitutes a major part of nematology, more appropriately, agricultural nematology. The entomoparasitic forms are often referred to as entomogenous (Greek *entomon* = insect, *genés* = born), entomophagous (Greek *phagein* = to eat) or entomophilic (Greek *philein* = to love) nematodes. These words are misnomers for Tylenchida which are truly parasitic in habit and therefore I prefer to call them entomoparasitic.

In entomoparasitic forms (Hexatylinea), only the gametogenetic female is parasitic, other stages in the host are transient and males rarely occur inside the host to fertilize the females of the second generation (*Parasitylenchus*). Occasionally, males and females may occur and mate inside the body of the mother nematode (*Scatonema*). Most of the entomoparasitic Tylenchida leave their hosts as juveniles or eggs to develop in the outside environment. The fertilized female seeks out and penetrates a host's larva or pupa to establish itself in the haemocoel. Several entomoparasitic genera have free-living mycetophagous (fungus-feeding) generations as well (see Fig. 3(a)).

Anguinoidea, a large group of Tylenchina, are close relatives of Hexatylinea but they lack the entomoparasitic phase and are totally mycetophagous and/or phytoparasitic; only the subfamily Sychnotylenchinae is found in association with insects. Another family, Halenchidae, has representatives exclusively parasitizing

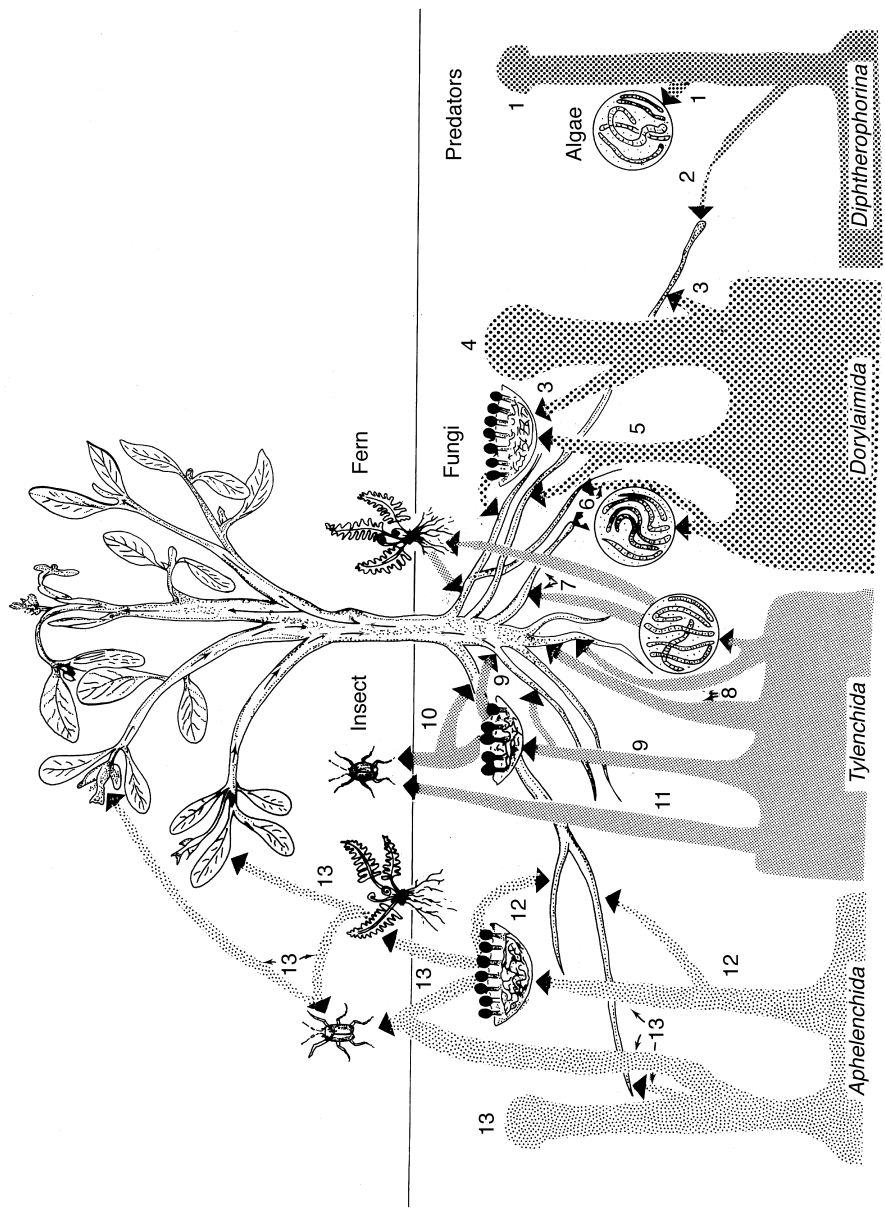
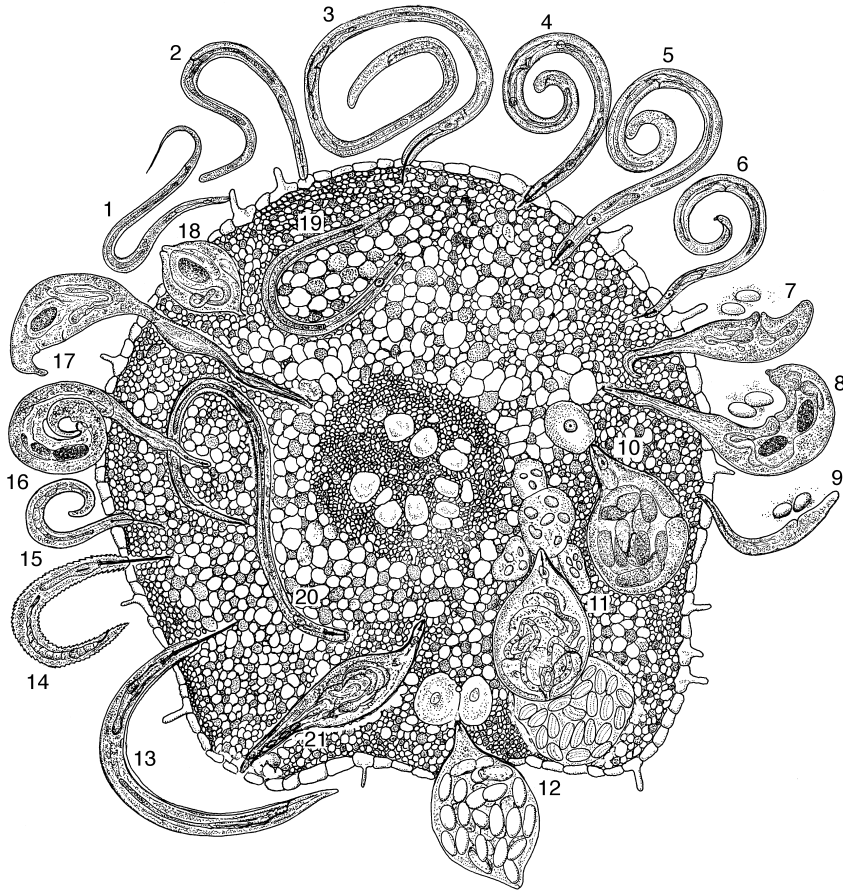


Fig. 1. Evolution of plant-parasitism in nematodes. Knobbed ends represent predators. Numbered evolutionary lines refer to the following taxa. 1. Diphtherophoroidea. 2. Trichodoroidea. 3. Dorylaimoidea (*partim*). 4. Nygolaimoidea, Aporcelaimidae, Discolaimidae. 5. Tylencholaimoidea. 6. Longidoroidea, Dorylaimoidea (*partim*). 7. Tylenchoidea. 8. Dolichodoroidea, Hoplolaimoidea, Cricematina. 9. Anguinoidea. 10. Neotylenchoidea. 11. Sphaerularioidea, Itonchoidea. 12. Aphelenchoidea, Aphelenchoidea. 13. Aphelenchoidea. (After Siddiqi (1983), courtesy The Systematics Association.)



**Fig. 2.** Diagrammatic presentation of various types of tylenchid nematode feeding on root tissues. 1. *Cephalenchus*. 2. *Tylenchorhynchus*. 3. *Belonolaimus*. 4. *Rotylenchus*. 5. *Hoplolaimus*. 6. *Helicotylenchus*. 7. *Verutus*. 8. *Rotylenchulus*. 9. *Acontylus*. 10. *Meloidodera*. 11. *Meloidogyne*. 12. *Heterodera*. 13. *Hemicycliophora*. 14. *Macroposthonia*. 15. *Paratylenchus*. 16. *Trophotylenchulus*. 17. *Tylenchulus*. 18. *Sphaeronema*. 19. *Pratylenchus*. 20. *Hirschmanniella*. 21. *Nacobbus*.

seaweeds and which are the only known plant-parasitic Secernentea flourishing in the sea (see Fig. 3(b)).

Tylenchida occur in all possible habitats in soil, water and plants. Their greatest diversity of form occurs amongst parasites of roots. A handful of moist soil from the rhizosphere of any plant should normally yield more than one species. A grain of galled wheat might contain up to 30,000 nematodes. One gram of coconut roots could yield about 4000 *Radopholus similis* (including eggs) (Koshy *et al.*, 1976). Andr ssy (1992) compared the species of Tylenchida with other soil-inhabiting nematode orders, and added: 'In free-living continental [vs. marine] nematodes the richest orders are the Tylenchida (2240 species, 40%), the Dorylaimida (1880

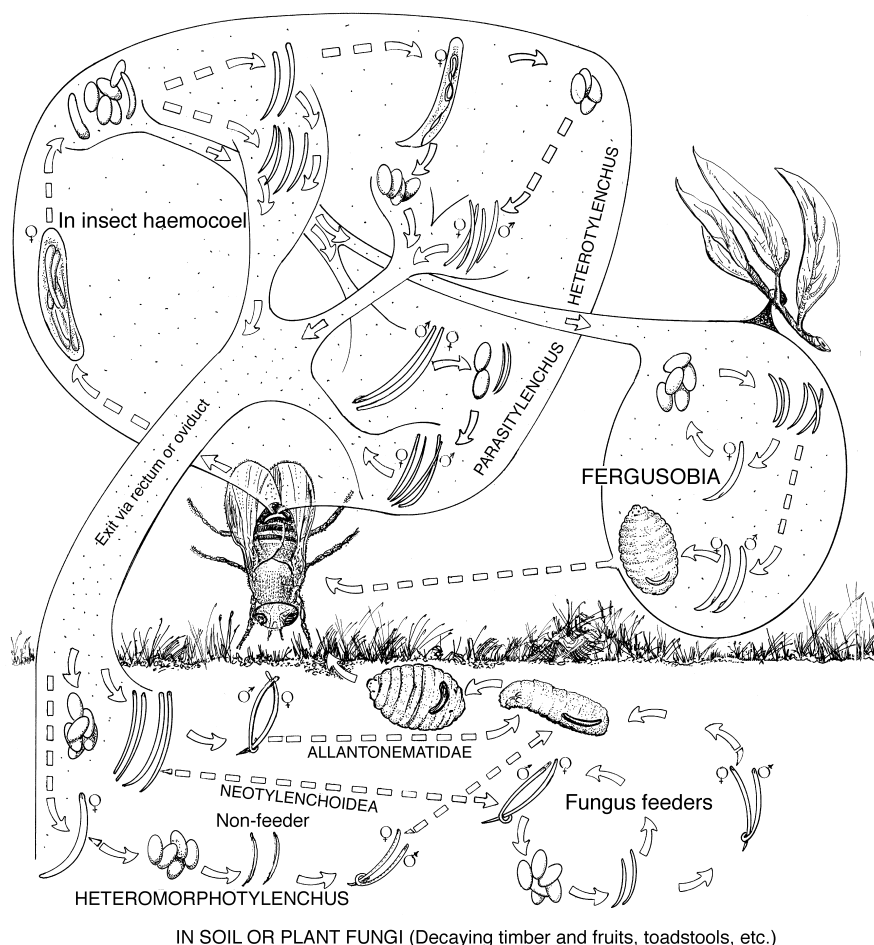


Fig. 3(a). Hexatylini. Radiation and life cycles of entomoparasitic forms.

species, 34%) and the Rhabditida (870 species, 16%). The Enoplida are represented by hardly 6% and all the Torquentia by less than 5% of species.'

Most of the Tylenchida are ectoparasites that live in soil and feed on roots, often changing feeding sites. Others have developed a closer association with the roots by becoming migratory or sedentary endoparasites. Only Anguinoidea and some free-living generations of insect parasites enter shoots, where they generally incite galls. Some entomoparasitic genera (e.g. *Deladenus*, *Fergusobia*) reach the tree tops as 'flying nematodes', transported there by their insect hosts.

Tylenchid nematodes move slowly in soil, water or plant tissue and, unlike predatory and saprozoic forms, do not jerk or twitch their head end or body. Their movement may be random or oriented towards the source of a stimulus. Plant-parasitic Tylenchida have a high sensitivity to the perception of stimuli (Prot, 1980). They are sensitive to low chemical gradients (e.g. where the highest concentration is

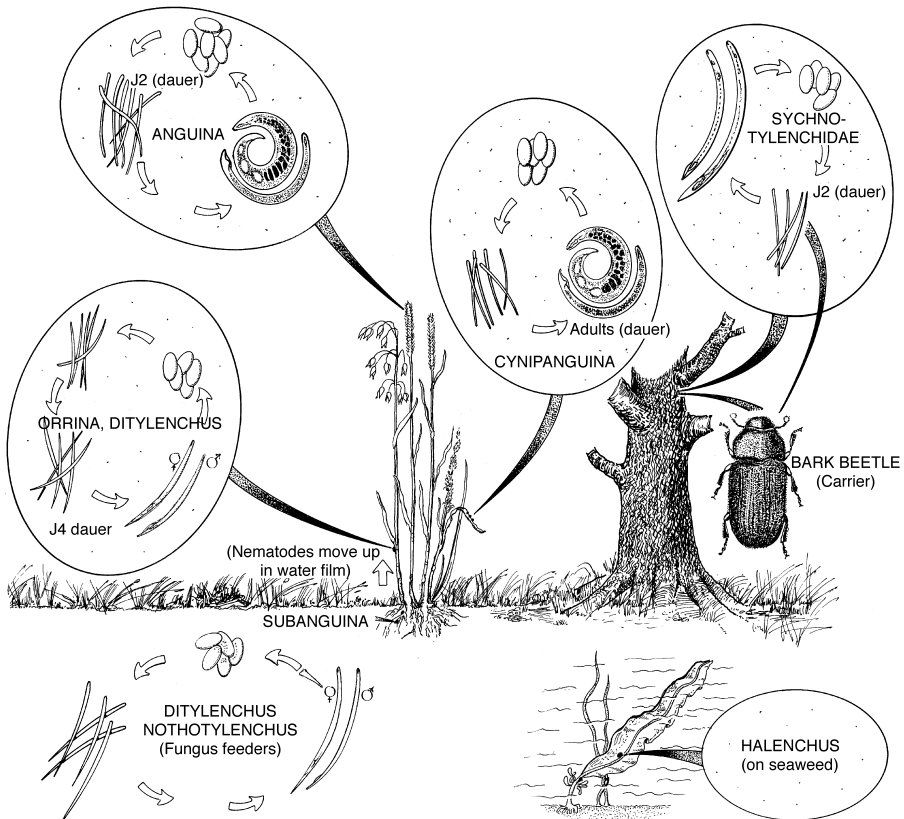
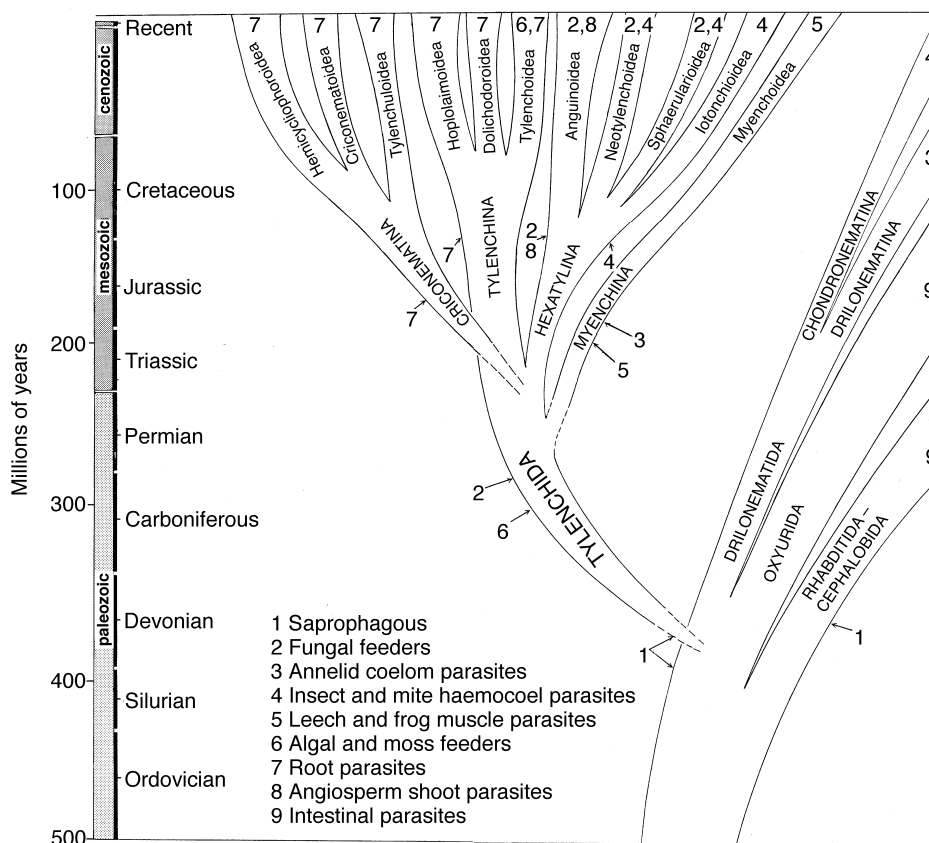


Fig. 3(b). Anguinata. Radiation and life cycles of fungus-feeding and plant-parasitic forms.

only  $10^{-3}$  M per litre), to a  $\text{CO}_2$  gradient with a concentration difference of 0.08% per cm and to a temperature gradient of  $0.033^\circ\text{C}$  per cm. This sensitivity might possibly be exploited by finding a chemical which can block the neuroreceptors of nematodes and thus reduce their chance of locating and invading the host tissue. Nematode dispersal is mainly by water, wind and transportation by man and animals. Irrigation waters can provide an annual inoculum of  $0.144 \times 10^6$  to  $15.362 \times 10^6$  plant nematodes per hectare (Faulkner & Bolander, 1970). Tylenchida are easily transported to other places by water, wind and human activity. Several Tylenchida were collected from dust deposits after a dust storm and which had entered anhydrobiosis and survived for one year (Gaur, 1989).

The nematodes that browse on roots for a short time, feeding on root epidermal and hair cells, have been called free-living (Jones, 1956) and non-parasitic plant-feeders (Yeates, 1971). According to Nicholas (1975), only those nematodes which have close adaptive morphological and physiological associations with host plants should be called parasites. A parasite has a physiological association with its host and completely depends on it for food, water and other physiological requirements. Strict application of Smyth's (1962) and Rogers' (1962) concepts of parasitism to



plant-feeding nematodes would, therefore, include only some nematodes (e.g. Heteroderidae, Tylenchulidae (see Fig. 6)), but not all stages of such nematodes are parasitic. Siddiqi (1983a) referred to this problem and preferred to call all plant- or fungus-feeding Tylenchida 'plant parasites'. In many groups males lack a stylet or have only a degenerated one and cannot feed, hence the female stage is the parasitic stage and is the basis for most descriptions and diagnoses of taxa in this book.

There is some evidence that several highly adapted root parasites (e.g. Heteroderidae) have co-evolved with their hosts (Krall & Krall, 1970; Stone, 1979). Tylenchida have a long history of about 400 million years, having supposedly originated in the Devonian Period of the Palaeozoic Era (Maggenti, 1971; Siddiqi, 1980, 1983a). Early Tylenchida must have been bulk feeders on bacteria, fungi and algae with their stylet-like stoma. Later, with the advent of the protrusible stylet, they evolved as parasites of rhizoids and roots (Tylenchina, Criconematina), as fungal feeders (Anguinata, some stages of Hexatyline) and as parasites of insect and mite haemocoels (Hexatyline) (see Fig. 4).

Tylenchida are also a source of food for soil microfauna, fungi and microorganisms. Protozoa (amoebae), nematodes (diplogasterids, dorylaims, mononchs), tardigrades, copepods and mites are predators on members of Tylenchida. About 150 species of fungi feed on these nematodes and an equal number of fungi are food for them. Several plant-pathogenic bacteria and fungi interact with the Tylenchida to produce severe symptoms of disease in plants, nematodes often predisposing normally resistant plants to bacterial or fungal attacks. Obligate parasites of nematodes, such as *Pasteuria penetrans* (= *Dubosquia penetrans* Thorne; *Bacterium penetrans* (Mankau)), have great potential in the management of plant-parasitic nematodes.

In zoological terms, Tylenchida are bilaterally symmetrical (even though some parts are radially symmetrical), elongate-cylindroid, unsegmented pseudocoelomate animals covered with a cuticular exo-skeleton secreted by the hypodermis (= epidermis). They have longitudinal muscles for locomotion, a terminal oral opening surrounded by bilaterally or radially arranged sensilla, protrusible stomatal stylet (see Fig. 7), a substylet orifice of the dorsal oesophageal gland, a circum-oesophageal or circum-intestinal nerve ring, an excretory system with a single duct and renette cell, a pore-like anus directed outward (Fig. 5), a true tail (postanal continuation of the body), and they lack a circulatory system and motile cilia. They are phasmidians but the suborders Tylenchina, Hexatylinea and Criconematina do not have detectable phasmids.

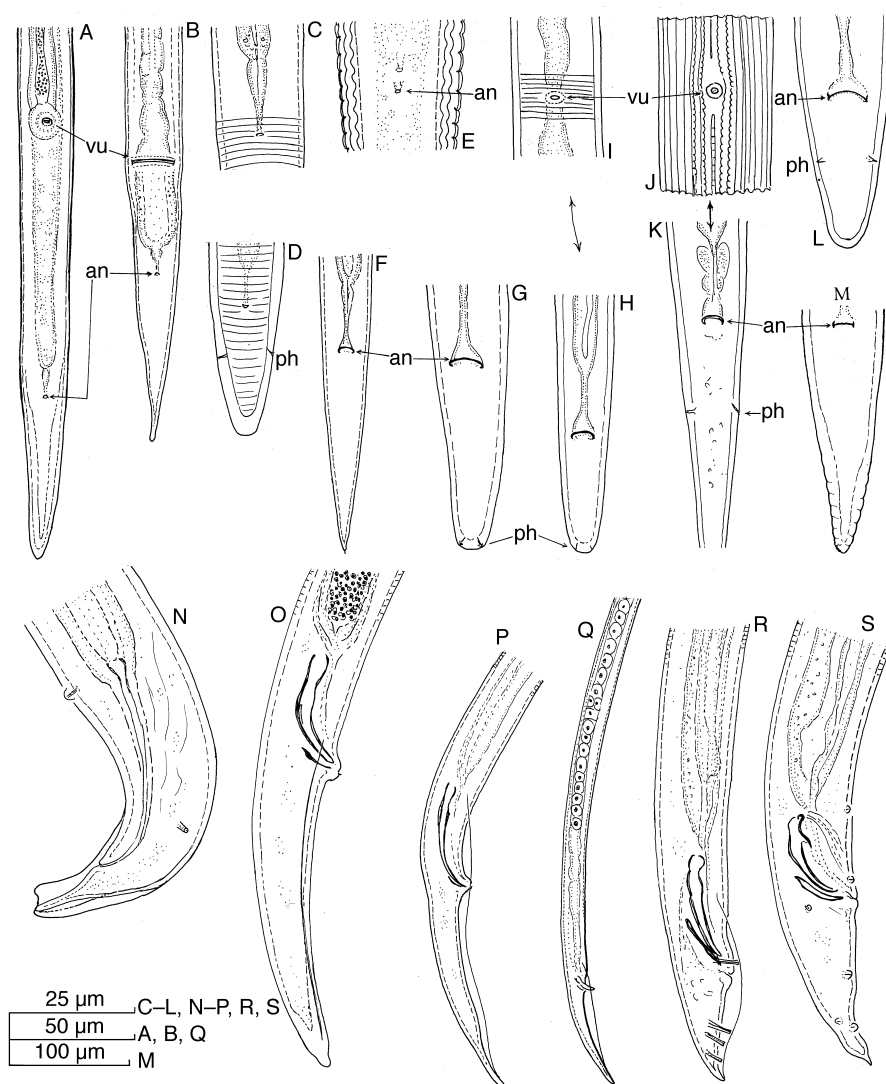
As in other nematodes, the sexes are separate and reproduction is by amphimixis, but autotoky (mainly parthenogenesis) is not uncommon; regeneration or asexual reproduction does not occur in nematodes. The gonads are tubular and outstretched (only secondarily reflexed or coiled). The male accessory genital structures include a pair of cuticularized spicules, a gubernaculum with or without telamon and titillae, a non-papillary (non-ribbed) bursa and genital papillae, 1–4 being grouped around the cloacal aperture; the male tail is devoid of caudal papillae.

The eggs are typically oval without spines, plugs or excrescences. The uterine egg is semifluid and can pass through a small hole. Advanced tissue parasites produce a much larger number of eggs than the surface root browsers and fungal feeders. Most Tylenchida are oviparous but a number of entomoparasitic genera have ovoviviparous species in which the eggs hatch in the uterus. Occasionally, in oviparous females the eggs hatch in the uterus and kill the mother, a phenomenon called *endotokia matricida*. The juvenile may hatch by cutting the egg-shell with its stylet (Doncaster & Shepherd, 1967) or by rupturing the egg-shell with its tail tip as in *Heterodera iri* (Laughlin *et al.*, 1974) or through normal rupture of the egg-shell due to the juvenile growth and movement. The juvenile develops to adult through four moults, the first moult normally occurring within the egg.

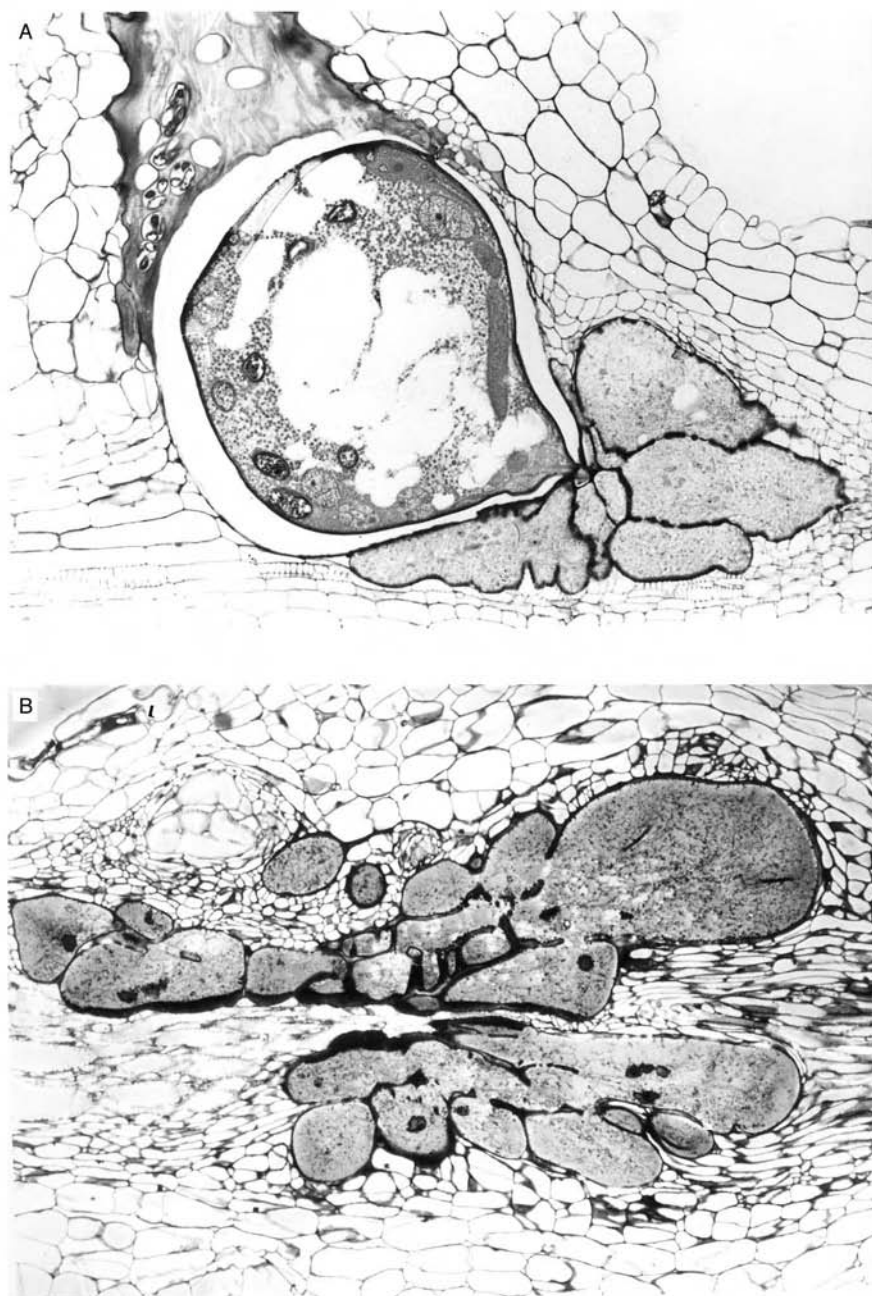
The nematodes which live in soil and are mobile in every stage are **necrotrophic**, whereas those that live in roots as sedentary parasites are **biotrophic**. The biotrophic nematodes such as *Heterodera* and *Meloidogyne* live as parasites within the root tissue. A special physiological relationship develops between them and the host tissue. As a response to their feeding on cells, the host plants induce the formation of nurse cells, giant cells or syncytia (Fig. 6). Such nematodes use special fine tubes formed by their salivary secretion/host response to feed from the nurse cells.

Some Tylenchida show a great ability to withstand desiccation and extreme adverse environmental conditions. The phenomenon of **anabiosis** (cryptobiosis) is

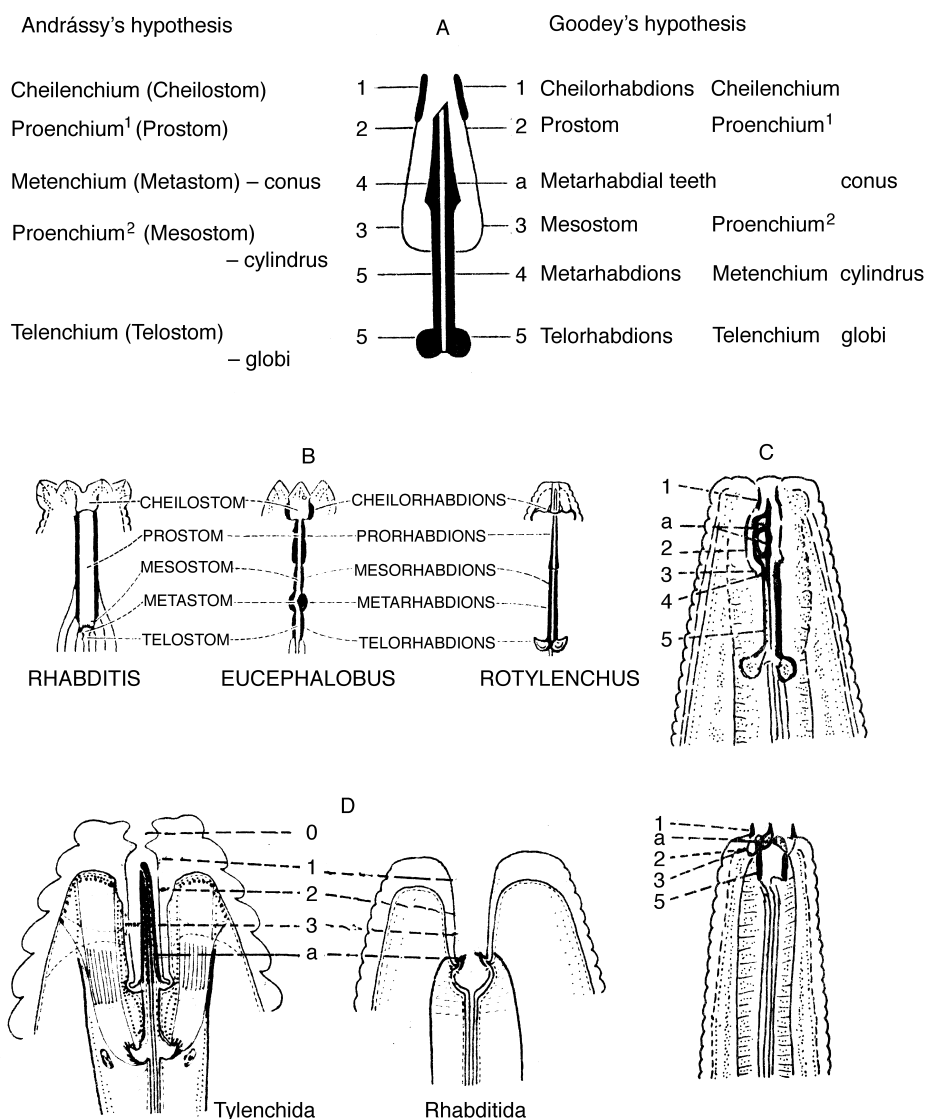




**Fig. 5.** Female anal apertures and male accessory genital structures in Tylenchida and other orders. A–M. Females. N–S. Males. A and B. Posterior ends showing vulva and anus. C–H and K–M. Tail ends showing anal aperture in ventral view. I and J. Vulva in ventral view. Hexatylini: A and O. *Sphaerularia bombi*. B. *Hexatylus viviparus*. Tylenchina: C. *Tylenchus davainei*. Q. *Ditylenchus* sp. Hoplolaimina: D. *Pratylenchus brachyurus*. Criconematina: E. *Hemicyclophora conida*. P. *Tylenchocriconema alleni*. Aphelenchida: F. *Aphelenchoides besseyi*. G and S. *Paraphelenchus myceliophthorus*. I, H and R. *Aphelenchus avenae*. Diplogasterida: J and K. *Tylopharynx* sp. Cephalobida: L. *Acrobeloides* sp. Oxyurida: M. *Lablostomum* sp. N. Unidentified Oxyurida. an = anus, ph = phasmid, vu = vulva. (After Siddiqi, 1980.)



**Fig. 6.** A. Syncytia (giant cells) formation in tomato root due to feeding by *Meloidogyne incognita*. B. Syncytia formation in potato root due to feeding by *Globodera rostochiensis*. (Courtesy U. Wyss, Germany.)



**Fig. 7.** Homologies of the stylet parts. A. Comparison of the hypotheses of Andrassy (1962) and Goodey (1964), after J.B. Goodey (1964). B. After Thorne (1961). C. Stoma parts of *Tylopharynx* sp. (upper) and *Mononchoides* sp. (lower), after Siddiqi (1980). D. After De Grisse (1972). 0, prestoma; 1, cheilorhabdions; 2, prorhabdions; 3, mesorhabdions; 4, metarhabdions; 5, telorhabdions; a, metarhabdial teeth.

well illustrated by members of the Anguinoidea. Fielding (1951) found that dormant *Ditylenchus dipsaci* and *Anguina tritici* could be revived after 20 and 28 years, respectively. The Tylenchida also provide good teaching and demonstration material for plant and insect parasitism, the process of metamorphosis (e.g. the development of

the *Heterodera* male, or *Hemicriconemoides* female) dimorphism and sex reversal. Morphology, organ systems, embryology, moulting and life cycle can easily be demonstrated to students (Siddiqi, 1966). Some Hexatylinea are remarkable for the alteration of mycetophagous and entomoparasitic generations, and for the polymorphism with di-, tri- or tetramorphic females. Hexatylinea and Anguinata have the advantage that they are easily cultured on fungi in agar medium and stocks are readily available for demonstrations and experiments.

The plant-parasitic genera, particularly *Heterodera*, *Globodera*, *Meloidogyne*, *Pratylenchus*, *Radopholus*, *Rotylechulus*, *Ditylenchus*, *Anguina* and *Tylenchulus*, cause significant losses to crop production. Rice, wheat and potatoes, which are the world's most important staple food crops, lose 10, 7 and 12% of production, respectively, due mainly to Tylenchida species (Sasser & Freckman, 1987). Forty species of Tylenchida have been listed as major pests of major mandatory crops (e.g. wheat, maize, sorghum, potato, banana, soybean, chickpea, pigeonpea, groundnut and beans) of the International Agricultural Research Centres of CGIAR (Consultative Group on International Agricultural Research) (Sharma *et al.*, 1997). These Centres – International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), International Institute of Tropical Agriculture (IITA), International Rice Research Institute (IRRI), International Centre for Agricultural Research in Dry Areas (ICARDA), Centro Internacional de Agricultura Tropical (CIAT), Centro Internacional de la Papa (CIP) – have made significant contributions to survey, evaluation of the nematode potential as crop pests, screening and making available resistant or tolerant species germplasms, suggesting effective control measures and making governmental and funding agencies aware of the nematode threat to their mandate crops.

The potential of Tylenchida as research models is considerable for work on biodiversity, ecology, physiology, embryology, neurobiology, cytogenetics, ageing, etc. So far, the nematodes most commonly used as models are either free-living Rhabditida (*Caenorhabditis elegans*, *C. briggsae*, *Turbatrix aceti*) and Cephalobida (*Panagrolaimus redivivus*, *P. silusiae*) or animal parasites.

Sohlenius *et al.* (1997) estimated mean nematode abundance of  $9.4 \times 10^6 \text{ m}^{-2}$  in an ombrotrophic mire at Abisko in northern Sweden. The nematode community comprised 34 nematode taxa and was typical for polar tundra soils. In a tropical rainforest at Mbal Mayo, Cameroon, carbon fluxes ( $\text{CO}_2$  and  $\text{CH}_4$ ) from the forest floor, could account for a high nematode abundance averaging  $2.04 \times 10^6 \text{ m}^{-2}$  (Lawton *et al.*, 1996). In Korup National Park, Cameroon, Price & Siddiqi (1994) found on average 4.4 million nematodes  $\text{m}^{-2}$  of which 33% were rhabditids and cephalobids, 23% tylenchids and 13% dorylaimids; the most diverse orders were the Dorylaimida (65 species-types) and the Tylenchida (35 species-types).

Since Tylenchida maintain a somewhat balanced community structure in the rhizospheres in non-agricultural lands, grasslands, forests and aquatic habitats, and are affected by changes in the environmental conditions, they serve as useful tools in ecological studies and can be used as models in environmental research for monitoring pollution. Price & Siddiqi (1994) stated: 'This suggests a role for the study of plant and soil nematodes in investigating, quantifying and monitoring past, present and future environmental changes. Such works could be restricted to species of the Tylenchida (due to their diversity and potential economic importance) and of the

Dorylaimida (due to their potential ecological significance). Both groups are well investigated taxonomically (Siddiqi, 1986; Jairajpuri & Ahmad, 1992) and nematology has the potential to make significant contributions of immediate relevance. The plant and soil nematode community of the Korup [forest] shows abundance, diversity and complexity features so characteristic of tropical rainforests. Only more research can establish both the ecological role and importance of nematodes and the contributions nematodes can make to our further understanding of the rainforests.'

Many important plant-parasitic nematodes have been spread by man (e.g. *Radopholus similis*, *Heterodera avenae*, *Globodera rostochiensis*, *Tylenchulus semipene-trans*, *Ditylenchus dipsaci*, etc.), but many are still confined to their areas of distribution (*Nacobbus aberrans*, *Meloidodera* spp., *Meloidogyne naasi*, *Pratylenchus goodeyi*, *Rotylenchulus* spp. (other than *R. reniformis* and *R. parvus*), *Ditylenchus angustus*, *Pterotylenchus cecidogenus*, *Heterodera glycines*, *H. oryzae*, etc.). The introduction, establishment and spread of dangerous parasites, predators, pests, and pathogens which are injurious to plants and plant products should be properly regulated and subjected to plant quarantine measures. Pest risk analysis of nematodes is the first step in the application of plant quarantine to promote plant protection (Siddiqi, 1986a). The nematode species dangerous to plants are called A1 category pests if they are not present in a country, and A2 category pests if present and localized in the country. A1 and A2 category plant nematode pests for European region have been listed and nematode data sheets produced by European and Mediterranean Plant Protection Organization (EPPO) and ASEAN (Association of South East Asian Nations) countries. CABI/EPPO (1997) have produced data sheets on quarantine pests including several Tylenchida species, for the European Union and for EPPO. Another example of international collaboration, cooperation and coordination in plant quarantine is the Inter-African Phytosanitary Commission which has a mandate from the Organization of Africa Unity.

Plant-pathogenic nematodes justify post-entry quarantine procedures as well as equivalent checks before export (OEPP/EPPO, 1990). Only material for scientific purposes should normally be imported. The simplest practical measure is to restrict the importation of soil (as such or accompanying plants, tools or packing material). UK plant health measures are based principally on the Plant Health (Great Britain) Order 1993 implementing European Union Directive 77/93/EEC, as amended. Several Tylenchida of quarantine status, e.g. *Ditylenchus dipsaci*, *D. destructor*, *Globodera pallida*, *G. rostochiensis*, *Radopholus similis*, etc. are covered by it. EU marketing schemes require visual freedom from quality-affecting nematodes. Soil samples normally comprising 500 g of soil from 100 cores per 4 ha (or less) are tested for freedom from *Globodera* spp. and virus vector nematodes (*Xiphinema*, *Longidorus* and *Trichodorus*) under certain certification schemes and, where necessary, for export crops (Ward & Hockland, 1996).

To control plant-parasitic nematodes, crop management, cultural practices and organic soil amendments are being favoured over chemical control on pollution strategy and high cost. Non-chemical control of plant-parasitic nematodes involves cultural practices such as crop rotation, fallowing, ploughing after irrigating, and developing resistance in plants, growing non-host and trap plants, growing seedlings in clean soil, paring infested corms, rhizomes and using clean seeds, applying organic

soil amendments such as oilcakes, chopped leaves and other plant material, soil and marine algae, solarization, immersing planting material in hot water to kill infesting nematodes, control of weeds and other host plants on which the plant nematodes may survive, etc. Applying regulatory control for exotic nematodes not reported from the area, health certification of all plant materials imported or exported from the country and monitoring and alerting for the dangerous nematode pests are of utmost importance.

The biological control agents such as nematode-trapping fungi, rhizosphere bacteria, egg-parasitic bacteria, predatory nematodes, insects and mites are useful to check crop damage, particularly over long periods, as they build up their populations in the soil. Considerable work has been done on *Pasteuria penetrans*, nematode-trapping fungi, such as *Arthrobotrys oligospora*, *Dactylaria* spp. and *Dactylella* spp., and antagonistic fungi, *Verticillium chlamydosporium*, *V. udum*, *Trichoderma harzianum* and *Paecilomyces lilacinus* but biopesticides using such agents have not yet been successfully applied in the field on a large scale. The main drawbacks are that the biopesticides or biological nematicides are difficult to produce and maintain long enough for economic effect (see Stirling's (1991) book for details on biological control). Several nematologists are now researching biological control of insect pathogens using species of *Deladenus*, *Steinernema*, *Heterorhabditis* and Mermithidae by studying their biology, ecology, distribution, multiplication, storage and formulations to be used in the fields as biopesticides. These nematodes have capabilities of evading insect defences and penetrating into the insect haemocoel. Steinernematids introduce entomopathogenic bacteria, e.g. *Xenorhabdus* spp., into insect pests, which ultimately kill them.

Because of their ability to sterilize or kill insect pests of agricultural importance, entomoparasitic Tylenchida have the potential to control insect pests of agricultural importance. The siricid wood wasp, *Sirex noctilio*, parasitic on pine trees (*Pinus radiata*), has been controlled and tree mortality reduced by the field application of *Deladenus siricidicola* as a biological control agent (Bedding, 1984). *Paraiotonchium autumnale* is another entomoparasite which has biocontrol potential for controlling *Musca autumnalis*, the face fly of range cattle, in North America (Kaya, 1993). *Orrina phyllobia* is showing promise in controlling *Solanum elaeagnifolium* (silver-leaf nightshade), a noxious weed infesting more than 1.2 million hectares of crop land in the USA.

The cruciferous host plant, *Arabidopsis thaliana*, is considered an ideal plant to study host-parasite relationships particularly at the genome level. The plant has a haploid chromosome number of 5 and its nuclear genome of about 70,000 kb is the smallest known among flowering plants (cf. wheat genome with 5,900,000 kb). A multinational coordinated genome project using *A. thaliana* has been set up to identify and characterize the structure, function and regulation of genes, to develop technologies for plant genome studies and to establish biological resource centres (Wyss & Grundle, 1992).

The diversity of form exhibited by Tylenchida demands a careful study of their morphological characters for the separation of genera and species. Good diagnostic characters should vary little within a taxon, but more between the taxa. The task of a taxonomist is not only to identify and describe new and known genera and species but also to try to explain how these taxa are related to each other and how they fit

into a system of classification. The species are based on populations of living or dead individuals, but genera and higher categories are abstract, with vague boundaries and limits set by the individual experience and concept of taxonomists. Due care must be taken when proposing new genera and higher categories.

When a large number of species occur in a genus, and more is known about their structural variability, generic boundaries become diffuse and, sometimes, it is necessary to shift or regroup species. This may involve removing some species to other genera (transfers) or to new genera (by splitting the old ones), as has happened with the genera *Tylenchus*, *Tylenchorhynchus* and *Criconemoides*, or enlarging the genus by emending its generic diagnosis (lumping) so that different groups (subgeneric) of species can be accommodated under it, as is done in this book with *Neodolichorhynchus*, *Criconema*, *Ogma* and others. Even so, large generic groups with many species still remain, in which splitting has not been tried, e.g. *Helicotylenchus*, or has proved unsuccessful, e.g. *Basiria*.

In this book, several genera have been recognized at the subgeneric rank rather than listing them under their senior genus name. This should help the users of the book who are mostly concerned with the identification and systematic position of genera and species. Identification and systematics go hand-in-hand. It is hoped that the subgeneric categories, as used in this book, will help in understanding the diversity and inter-relatedness of taxa to be useful in identification, as well as in indicating the probable lines of evolution of various species.

The generic and subgeneric categories do help in building a sound system of classification of species. Although genus and subgenus names are of coordinate status, the citation of a subgenus name within brackets between the genus and the species name neither affects the binomen nor makes the name a trinomen. For example, the name *Malenchus* (*Neomalenchus*) *ovalis* is the same as *Malenchus ovalis*. However, the name *Malenchus* (*Neomalenchus*) *ovalis* does indicate that the species epithet *ovalis* has been combined with *Neomalenchus* and that it lacks a muscular median oesophageal bulb which helps in active feeding. Other examples of subgeneric names are found in the genera *Rotylenchus*, *Hoplolaimus*, *Ogma*, etc.

Some genera (*Aerotylenchus*, *Afrina*, *Basiroides*, *Bidera*, *Mulveyotus*, *Sherodera*, *Zelandodera*, etc.) considered here as junior synonyms may in future be shown to be valid. Similarly, some of the genera treated here as valid may later prove to be junior synonyms, on the basis of new ideas and interpretations of distinguishing characters. There are taxa of uncertain position, e.g. *Paurodontidae*, and genera dubia of *Hexatylna*, which may prove to be senior synonyms. There are also anomalous genera (e.g. *Meloidoderella*) whose status can be determined only after the type-material is refound or topotypes are collected and restudied.

The number of valid genera in Tylenchida considered in this book is 225 including 21 considered as subgenera, three considered as *genera dubia* of uncertain position and another three as *genera inquirenda* needing further study. There are 105 genera listed as invalid synonyms. The number of valid species in Tylenchida considered in this book is 2828, the number of synonym species is 413 and the number of *species inquirendae/dubiae* is 163.

Diagnoses and differential keys are provided for all valid genera. In most cases diagnoses have been enlarged. To avoid confusion with related genera in other subfamilies, some familial characters are repeated in generic diagnoses. Data for the type species, especially the type host, habitat and locality, are frequently mentioned

and etymologies of the generic names provided. In the diagnoses of taxa, if the sex or developmental stage is not mentioned, the morphological or ecological characters refer to the female since the female is the parasitic stage both as plant and insect parasite; males and juveniles of some groups have a degenerated oesophagus and cannot feed.

The ICZN Article 23(c) dealing with the Principle of Priority states: 'The priority of the name of a taxon of the family group, genus group, or species group is not affected by elevation or reduction in rank within its group'. Accordingly, in this book, names of authority and year of taxa have been cited as required by the Article, but the authority and year of the first elevating or lowering of the ranks have also been added within the brackets immediately after the citations.

Since new species and genera are constantly being described, most systems of classification soon become unstable due to the variability in structure, and also because their proposers may have failed to consider the likely phylogenetic relationships, may have interpreted homologies wrongly or may not have had a wide enough spectrum of data. Such systems invariably lack predictability, so that the characters used to specify groups will not remain congruent and parsimonious when new characters and taxa are discovered. Nevertheless, the various systems of classification proposed thus far for the Tylenchida have created new knowledge and interest which are so necessary for the progress of systematics.

As for other animals, the phylogenetic histories of Tylenchida can never be correctly stated because there are no fossils and also because the evolutionary pathways of animals can only be inferred. Yet, to achieve a sound and stable classification, modern methodologies of systematics, i.e. evolutionary, cladistic and phenetic, have to be properly used. Homologies (both structural and behavioural) as correspondences in characters and character states should be determined and interpreted to show the possible origin and evolutionary line of the taxa concerned. In addition, the chemical, cytogenetic, embryological and numerical taxonomic data have to be analysed before we can truly understand the diversity of Tylenchida and have a meaningful and stable classification.

It is now more than 50 years since Thorne (1949) proposed the order Tylenchida and gave a system of classification for it. Since then, hundreds of new species and scores of new genera have been discovered and a great deal of information on nematode morphology and characterization has been accumulated, necessitating changes in this system. In fact, several new systems have since been proposed. Important ones are those by Allen & Sher (1967), Golden (1971), Siddiqi (1972, 1986), Andr  ssy (1976), Fotedar & Handoo (1978), Maggenti (1981), Ryss & Krall (1981), Luc *et al.* (1987) and Chizhov & Berezina (1988).

Although these systems have greatly augmented our knowledge of Tylenchida, a sound, stable and close to natural classification and one which is acceptable to most nematologists is still difficult to achieve. This is largely because disciplined clado-evolutionary methods have not been applied. Nevertheless, systems of classification have been changing for the better, and in many groups we have arrived at a point where many taxonomists are in some agreement.

Taxonomy at the grassroots is still somewhat unsatisfactory: the tug-of-war between the splitters and lumpers continues. I have tried to strike a balance between the conservatism of lumpers, who hate the so-called inflation in the num-



bers of higher categories, and the enthusiasm and liberalism of the splitters, who do not hesitate to propose families and genera based on characters which may be of generic and specific value only. My aim in writing this book is, therefore, twofold: firstly, to give diagnoses and differential keys for all the valid genera and higher categories of Tylenchida, including a list of all the nominal species under their respective genera; and secondly, to provide a system for their classification on as sound a basis as possible which is practicable, stable and has most predictive value. I believe that the system presented here is the best possible expression of the similarities of various taxa both phenetically and phylogenetically.

## 2. ABBREVIATIONS, SYMBOLS AND GLOSSARY

### Abbreviations and Foreign Words and Phrases Used in the Taxonomy of the Tylenchida

ap., apud	in the work of
Art.	Article (of the International Code of Zoological Nomenclature)
auct.	of author(s)
cf.	<i>confer</i> , compare
DO	dorsal oesophageal gland orifice
DN	dorsal oesophageal gland nucleus
DNA	deoxyribonucleic acid
mtDNA	mitochondrial DNA
ELISA	enzyme-linked immunosorbent assay
emend.	emended, emendation
<i>et al.</i>	<i>et alia</i> or <i>et alii</i> , and others
fam.	family
gen.nov., gen.n., n.g.	<i>genus novum</i> , new genus
gub.	gubernaculum
ibid.	<i>ibidem</i> (in the same place as above cited reference)
ICZN	International Code of Zoological Nomenclature, not used here for the International Commission on Zoological Nomenclature (I.Com.Z.N.)
incertae sedis	wrongly inserted, of uncertain position
<i>in litt.</i>	in correspondence
L	body length
L.	Latin or Linnaeus
lapsus calami	typists' or printers' error, an error in spelling in nomenclature
loc. cit.	<i>locus citatus</i> , local citation, as cited above
MAbs	monoclonal antibodies
no., n	number

nomen conservandum	conserved name. A name conserved by the use of the plenary powers of the Commission for Zoological Nomenclature, which otherwise would have been invalid using ICZN
nom. dub.	<i>nomen dubium</i> , dubious name which cannot be applied with certainty to any taxa, e.g. when the description is inadequate and the type specimens are unavailable
nom. nov.	<i>nomen novum</i> , new name, equivalent to new replacement name required for example by homonymy
nomen nudum (pl. nomina nuda)	naked name(s), invalid name(s) which is not an available name, but can be made available for the same or a different concept with the authorship and date from that act of establishment
nomen oblitum	forgotten name, which remained unused as senior synonym in primary zoological literature for more than 50 years, as per ICZN Article 23(b) of the I and II editions, but later omitted from the III edition
p. (pl. pp.)	page(s)
PAGE	polyacrylamide gel electrophoresis
part, partim	part, in part
PCR	polymerase chain reaction
pers. comm.	in personal communication
RAPD	random amplification of polymorphic DNA
RFLP	restriction fragment length polymorphism
RNA	ribonucleic acid
rRNA	ribosomal RNA
SD	standard deviation
SE	standard error
SEM	scanning electron microscope/microscopy
sensu	according to
sic	thus (an exact transcription)
s.l.	<i>sensu lato</i> , in a broad sense (cf. <i>sensu stricto</i> )
sp. (pl. spp.)	species
spic.	spicule
sp. inq.	<i>species inquirenda</i> , demanding further inquiry or study as the characters are insufficient for recognition
sp. n., sp. nov., n. sp.	<i>species nova</i> , new species
s.s., s.str.	<i>sensu stricto</i> , in the strict sense (cf. <i>sensu lato</i> )
st.	stylet
subfam.	subfamily

subsp., ssp.	subspecies
SVN	subventral oesophageal gland nucleus
SVO	subventral oesophageal gland orifice
taxa (sing. taxon)	taxonomic categories from subspecies to kingdom
TEM	transmission electron microscope/microscopy
<i>vide</i>	see

## Symbols

For symbols used in body measurements see pages 37 and 38.

## Explanation of Terms used in Taxonomic Works

**$\alpha$ -,  $\beta$ -, and  $\gamma$ -taxonomy** = in short, descriptive, synthetic and evolutionary taxonomy, respectively. Alpha taxonomy is the process of naming and describing species, and providing diagnosis, emendation, etc. of taxa, etc. Beta taxonomy includes revising and arranging taxa in higher categories that reflect evolutionary history. Gamma taxonomy deals with tracing intraspecific variation and establishing the evolutionary systematic lines, critical analysis of classification and publication of monographs and books on taxonomy.

**Agamospecies, morphospecies** = species that reproduce asexually, e.g. by parthenogenesis and are distinguished on morphological and not on gene-flow basis.

**Allopatry and sympatry** = taxa or populations that occupy geographically separate areas, and those that occupy the same geographical areas, respectively.

**Allozyme** = any variant of an enzyme coded by different alleles at the same gene locus (refers to motility variants identified by electrophoresis).

**Binomen, trinomen or scientific names** = binomen is the name of a species with two words, first of a genus name beginning with a capital letter and second of species name which is not capitalized, and trinomen is the subspecies name with three words, the last one of which is subspecific and is not capitalized. Specific epithet includes both species and subspecies names. Citation of subgenus name within brackets is not a part of either a binomen or a trinomen, but it does imply that the species name has been combined with the subgeneric name. Binomen and trinomen are called scientific names.

**Biodiversity** = diversity in number and kind of taxa and/or their combined genetic variations.

**Biological species** = a species in which gene flow occurs readily and frequently between its members, and not between its members and those of other species, i.e. such species are reproductively isolated from other species. In other words, a biological species is a group of interbreeding natural populations which have a similar genotype but which are reproductively isolated from other such groups.

**Biotypes, pathotypes and host races** = biological or physiological races of a species which can be differentiated on host reactions; they have no taxonomic status since ICZN does not recognize any taxa below the subspecies level.

**Character and character state** = any structure or behavioural system that is used to characterize a taxon, and any condition that a character can display, respectively.

- Clade and polyclade** = any supposedly monophyletic group in a phylogenetic analysis. Polyclade is used as a multiple-entry identification key in a computer or in punched cards.
- Cladogram, dendrogram and phylogram** = a cladogram is a dendrogram or tree diagram based on synapomorphies depicting a phylogenetic hypothesis. It only depicts the branching pattern of the evolutionary history and, unlike a phylogram, it does not indicate, by means of branch length, the degree of evolutionary change that occurred along each lineage.
- Clone, cloning** = a group of genetically identical organisms, resulting from non-sexual cell division. A number of copies of a fragment of DNA produced by cloning or amplifying the number of copies of DNA.
- Cluster analysis, OTUs and HTUs** = procedure that links operational taxonomic units (OTUs) into clusters on the basis of their attributes or overall similarities, as used in phenetics. HTUs are the hypothetical ancestral characters or character states used in a cladogram.
- Commonality principle, plesiomorphy and apomorphy** = the principle that plesiomorphies (primitive or ancestral characters or character states) will be commoner on average than apomorphies (derived character or character states).
- Compatibility analysis** = procedure for eliminating characters from a phylogenetic analysis on their not being consistent with other characters.
- Congeneric** = two or more species belonging to the same genus.
- Congruence** = degree of similarity between two phylogenetic systems or phylogenetic trees derived from different data sets.
- Cotype** = a paratype or syntype, not in usage now as it is not recognized by the ICZN.
- Dichotomy** = in a differential key where two new branches arise from one stem.
- Diploid, haploid** = during meiosis, the chromosome number of a diploid cell is halved,  $2n$  becomes  $n$ .
- Distance matrix** = a taxon-by-taxon matrix in which distance or dissimilarities are measured.
- DNA fingerprinting** = technique based on restriction fragment analysis of DNA that reveals polymorphisms at dispersed loci of tandemly repeated DNA, used for evaluating relatedness between closely related individuals.
- DNA hybridization** = process by which single-stranded DNA will pair with other homologous strands.
- Electrophoresis and electromorphs** = a process of separating molecules in a supporting medium on their electric charge in combination with other factors. Electromorphs are variants of a protein characterized by their motility properties during electrophoresis.
- Entomoparasites and phytoparasites** = parasites of insects (and, for practical purposes, mites) and of plants (and fungi), respectively.
- Family-group names** = any recognized taxonomic category name between genus and infraorder (tribe, subfamily, family and superfamily names). ICZN recognizes categories between superfamily and species only and does not cover taxa above superfamily rank.
- Genotype and type species** = the type species of a genus, genotype, is now obsolete since it causes confusion with genetic make-up.

**Genus-group names** = names of genus and subgenus categories; changing rank of a taxon within a genus group does not affect the authorship or year of publication.

**Gradualism vs. punctuated equilibrium** = a Darwinian evolution concept in which species are believed to have evolved through gradual change over time, as against punctuated equilibrium which postulates that new species appear by sudden jumps or saltations due to mutations during periods of rapid evolution separated by periods of relative constancy, and which gradually dominate or replace the mother species.

**Hennigian method** = using cladistic approach for defining taxa (clades) by synapomorphies as proposed by Hennig (1950, 1957, 1966).

**Heuristic** = method of progressive improvement of estimates by trial-and-error search rather than by following a set method. Also a method of algorithms for finding shortest trees, which are not guaranteed to represent the most parsimonious ones.

**Holotype, allotype and paratype** = a holotype is a member of a type series (the best example on which the concept of a species or type species is based, and it should be well preserved and preferably illustrated in the description); the remainder of the type series are paratypes; an allotype represents the opposite sex to that of the holotype, not in use since a type series includes only the holotype and paratypes.

**Homology and analogy** = similarities in characters or character states in two or more taxa that are the result of their inheritance from a common ancestor; analogy refers to the similarities which are not due to their inheritance from a common ancestor.

**Homonymy, primary and secondary homonyms** = either of two or more identical scientific names. When two identical names occur in a genus, the junior homonym has to be given a new name, called the nomen novum. Primary or secondary homonyms are the identical names that were proposed for different taxa in the same genus (primary homonym) or brought to the same genus (secondary homonym); secondary homonymy breaks by the transfer of a homonym to another genus.

**Homoplasy** = in phylogenetic analysis, when an additional number of character states resulting from reversals and parallel or convergent evolution are also considered, besides the minimum number of changes that could theoretically have taken place.

**Ingroup and outgroup** = in phylogenetic analysis, comparison with members of the same monophyletic group or with members of other such groups, respectively.

**Isoelectric focusing, isoelectric point** = electrophoretic separation of protein variants based on their migration within a pH gradient to their isoelectric points, where they accumulate (focus point).

**Isozyme, allozyme** = usually in electrophoresis, a form of an enzyme coded for by a gene at a different locus from that of another form of the same enzyme. Isozymes may arise, e.g. through gene duplication. An allozyme represents one or more variants of an enzyme coded by different alleles at the same gene locus.

**Karyotype** = chromosome complement of a cell or organism.

**Metaspecies, metataxon** = a species or taxon, respectively, which is only defined by symplesiomorphy and is not known to be paraphyletic.

- Metatype** = a specimen which has been compared with the holotype and believed to belong to the same species.
- Monoclonal antibody** = a pure antibody which is specific to a single antigen determinant and is produced from a specific clonal line of hybridoma cells.
- Monophyletic, holophyletic** = terms used for a taxon or group of taxa whose members are supposed to have descended from a common ancestor.
- Monothetic, polythetic** = to differentiate on one or many sets of characters, respectively, e.g. in a key.
- Monotypy** = monotypic taxon must be designated as type, e.g. when a species is described on a single specimen, it becomes the holotype.
- Name-bearing type** = in 1985 ICZN introduced this term to indicate either a type genus, a type species or any accepted type specimen which provides an objective standard for the application of a scientific name.
- Numerical taxonomy** = a numerical approach to taxonomy, generally applied to refer to phenetic methods involving clustering and classifying purely on similarity rather than phylogenetic grounds.
- Objective synonym** = when two or more named genus or species names are based on the same species or type specimens, respectively.
- Original designation** = designation or fixation of the type species of a genus in an unambiguous way in the original description.
- Paraphyletic, paraphyly** = a taxon or group of taxa supposed to have a common ancestor and defined by a unique apomorph (derived character state), but not all of whose members are included because some may have undergone one or more reversals of that apomorph.
- Parasites, pathogens and predators** = those (nematodes) that feed, develop and reproduce on their hosts and live at their expense; those that produce disease; and those that prey naturally on others and devour their body contents, respectively.
- Parsimony** = in cladism, the most likely phylogenetic explanation requiring the least number of evolutionary steps (i.e. the most parsimonious explanation).
- Patronym** = a scientific name based on a person, in his honour or in recognition of his work.
- Phenetics, phenon** = now used mainly to describe numerical taxonomy using clustering of taxa (phenons) based on similarity.
- Phylogeny** = the evolutionary history of a group of taxa.
- Polarity** = evolutionary direction of a character state transition, determining a plesiomorphic (primitive) or apomorphic (advanced, derived) state.
- Polymorphism** = occurrence of two or more phenotypic states of a character among the members of a taxon.
- Polyploidy, aneuploidy** = increasing of chromosome number above the normal diploid number ( $2n$ ) by an integral number of  $n$ , but this might have been modified subsequently to have a different (lower) number by aneuploidy.
- Restriction fragment length polymorphism (RFLP) and restriction enzyme** = the occurrence in a taxon of more than one morph defined by the presence or absence of a particular restriction enzyme recognition (cleaving) site. A restriction enzyme is one that cleaves double-stranded DNA.
- Sibling species** = very closely related species which differ only in minute or cryptic

morphological characters but which have different biological characteristics and are reproductively isolated.

**Species-group names** = names of species and subspecies; changing the rank of a taxon within a species group does not affect the authorship or year of publication.

**Subjective and objective synonyms** = synonyms are two or more generic or species names that can be applied to a single taxon. Subjective synonyms are those that result from the opinion of a person, seeing that they are in fact the same taxon described under different names. Objective synonyms result from two or more taxa having the same type (species or specimen) and over which there can be no difference of opinion.

**Symplesiomorphy and synapomorphy** = sharing of plesiomorphs and apomorphs, respectively.

**Syntype lectotype, topotype and neotype** = in a type series, if the holotype is lost, all the paratypes become syntypes, from which any one syntype can be chosen and named the lectotype, after which action all the syntypes become paralectotypes (or lectoparatypes). If the type series is lost, specimens of the species collected from its type host and locality are called topotypes, from which a neotype is selected and designated.

**Tautonymy** = identical spelling of two generic or species names.

**Taxon, plural taxa** = a group of organisms or a formal taxonomic unit at any level of hierarchic classification from subspecies to kingdom categories.

**Taxonomy and systematics** = these terms are largely synonymous. Taxonomy deals with identifying, naming and classifying organisms, whereas systematics has a broader definition and includes aspects of the phylogeny, evolution, biogeography, genetics and physiology of the organisms.

**Transformation series** = in phylogenetic analysis, a hypothesized set of likely transitions between multiple character states.

**Type series** = all the specimens of a species used at the time of its description.

**Voucher specimens** = specimens used in a study, which are not from a type series, and which are deposited in a permanent collection for later use or reference.

**Weighting** = assigning different importance or value to different character systems in phylogenetic analyses or identification systems (e.g. in keys).

### 3. HISTORICAL REVIEW

Historical perspectives of a science give an insight into man's eternal quest for knowledge and reveal how defective observations, interpretations and judgements are constantly being replaced by better ones. A scientific theory (a hypothesis when tested becomes a theory, which carries more weight) by its very definition is a falsifiable theory since it depends on many variables. The least falsifiable theory is the best theory, but a poor theory is always better than none, since it generates research. Divine revelations and scriptures as eternal truths (only their human interpretations are falsifiable), metaphysical concepts and philosophical idealism have greatly helped scientific pursuits over the ages, simply by providing the basic stimulus for using the most valuable of human assets – the imagination.

The science of nematology began in the 17th century, when the compound

microscope was discovered and the 'first nematologist', Petrus Borellus, looked with utter amazement on the 'little serpents' (= *Anguillula*) in table vinegar. The name *Anguillula* was followed by *Anguillulina* and the two names appeared in the literature for quite a long time but then suddenly disappeared from the scene with few nematologists knowing what actually happened to them. Today the 'little serpents' are made to look as large as a whale with the recent invention of the electron microscope.

The earliest known Tylenchida were highly adapted parasites, which were identified either by the disease symptoms they produced (*Anguina* in wheat-gall and *Meloidogyne* in root-gall) or by their miraculous parasitic adaptations (the everted uterus of *Sphaerularia* and the cyst of *Heterodera*).

The first member of the Tylenchida seen and reported was the wheat-gall nematode, *Anguina tritici*, by John Turbevill Needham (1743, published 1744) who wrote to the President of The Royal Society, London, stating that small black grains of smutty wheat had soft fibrous substances which, upon soaking in water, took life and yielded a large number of motile worms. Linnaeus (1767, *Systema Naturae*, p. 1326) under the genus *Chaos* wrote 'TRITICI Grana abbreviata illa & rotundata, exsiccata etiam post annos, in aqua tepidiuscula intra horulam egerminant in ascaridiformem quasi vermicucum; animatum vix dixero'.

Scopoli (1777) proposed the genus *Anguina* (original spelling *Angvina*; note that in Latin inscriptions u is often given as v) for the wheat-gall nematode, and 55 years after its discovery by Needham, the species was named *Vibrio tritici* by Steinbuch (1799) who also described *Vibrio agrostis* parasitizing seeds of bentgrass. In 1850 Hardy had recorded a species causing galls on grass leaves and called it *Vibrio graminis*. These *Vibrio* species were finally transferred to *Anguina*. A closely related species, *Anguillula dipsaci* (now *Ditylenchus dipsaci*) was reported from teasel, *Dipsacus fullonum* L. by Kühn (1857).

That Shakespeare's words 'sow'd cockle reap'd no corn' in *Love's Labour's Lost* (Act 4, Scene 3, line 379) refer to the wheat-gall nematode, as suggested by Thorne (1961), has been disputed by Southey (1972) who argued that Shakespeare used 'cockle' to mean a weed of the corn field (e.g. the corn cockle, *Agrostemma githago* L.), and that 'cockle' or 'ear cockle' as a description of *A. tritici* galls had not been in use before the middle of the 19th century.

The first insect-parasitic member of the Tylenchida was reported by Reaumur in 1742 which was probably *Sphaerularia bombi* (vide Nickle & Welch, 1984). The first Criconematina was described by de Man (1880) as a male *Macroposthonia annulata*; the generic name is feminine in gender but means 'large penis'. The first female Criconematina was named as *Dorylaimus giardi* (now *Criconema giardi*) by Certes (1889) who, in the same paper, described *Eubostriechus geurnei* (= *Criconema guernei*, the type species of the genus) as having a sting (= stylet).

During the middle of the 19th century, the root-parasitic Tylenchida were beginning to receive attention. In England, Berkeley (1855) observed 'Vibrios' (root-knot nematodes) in galls of a glasshouse cucumber. Similar nematodes were found in root-galls in *Dodartia orientalis* by Müller (1884) who called them *Heterodera radicola* by transferring the species described by Greeff (1872) as *Anguillulina radicola* to the genus *Heterodera*. Cornu (1879) in France described a new nematode, *Anguillulina marioni*, from root-knots on sainfoin (*Onobrychis sativus* Lam.). Goodey (1932) transferred this species to the genus *Heterodera* as *H. marioni*. The name *H.*



*marioni* was in use for a long time, and appears as such for the root-knot nematodes in Franklin's (1951) review of the genus *Heterodera*. Goeldi (1887, published 1892) had called the root-knot nematodes found on coffee in Brazil as *Meloidogyne exigua*. Chitwood (1949) clarified the status of the root-knot nematodes by reinstating *Meloidogyne* as the generic name for them. The genus *Caconema* Cobb, 1924 became a synonym of *Meloidogyne* but here it has been treated as an invalid senior objective synonym of *Subanguina* (see discussions under *Meloidogyne* and *Subanguina*).

In 1859, Schacht reported a serious disease of sugarbeet (Rübenmüdigkeit) in Germany. This was found to be caused by a nematode, *Heterodera schachtii*, named by Schmidt (1871). The genus *Heterodera* Schmidt, 1871 was thought to be preoccupied by the name *Heteroderes* Latreille, 1834 (Coleoptera) by Railliet (1896) who proposed a replacement name *Heterobolbus*, but this was rejected by Baylis & Daubney (1926) and cannot justifiably be used due to lack of homonymy.

After the discovery of wheat-gall nematode by Needham in 1743, Tylenchid nematodes received almost no attention from scientists for the next 150 years and, as put by Maggenti (1988), 'Rudolphi in 1809 discarded them from his classification because they were not intestinal parasites. They were moved and pushed for the next hundred years without thought or reason. For most of their history they were buried within the bacterial feeding rhabditids; a cemetery only recently revisited by Siddiqi (1986).'

By the turn of the 19th century, the taxonomy of Tylenchida had progressed far enough to stimulate scientists to attempt the construction of a hierarchic system of classification of known forms. By 1913, there were seven genera and a large number of known species of plant-parasitic nematodes. The early classification works were ill-coordinated and usually based on a single character for differentiation (the monothetic concept) which produced unstable classification. For example, the free-living nematodes were classified by Diesing (1861) under two families – Cirrhostomae and Anguillulidae – on the presence or absence of cirri or setae in the head region only. Eberth (1863) found this system unsatisfactory and proposed that Anguillulidae be recognized as lacking caudal glands, and that those possessing them be assigned to Urolabes. Rauther (1930) also used a single character, the presence of a rachis in the ovary, to characterize Rachidophora which proved to be a group of unrelated nematodes.

Early workers on Tylenchida studied either free-living and plant-parasitic nematodes, or insect parasites. The former produced excellent monographs, e.g. those by Bastian (1865), Bütschli (1873), Örley (1880), de Man (1880, 1884) and Cobb (1893), while the latter gave us such important genera as *Sphaerularia* Dufour, 1837; *Allantonema* Leuckart, 1884 and *Bradydema* zur Strassen, 1892. Fuchs (1914, 1915) initiated work on the taxonomy of the tylenchid parasites of bark beetles and published excellent papers on this group in 1929 and 1938. The dedication and hard work of Bastian, Bütschli, Örley, de Man, Filipjev, Micoletzky and Cobb laid strong foundations for the science of nematology through their major publications containing the descriptions, fine illustrations and well-attempted classifications of tylenchid and other nematodes.

Bastian (1865) produced an excellent monograph on Anguillulidae, describing 100 new species. Thorne (1961, p. 5) wrote that this publication marked the beginning of the science of nematology. Bastian (1865) realized that the collection and

naming of nematodes up to that time were insufficient for a philosophical classification to be attempted. Instead he gave tables to assist in their characterization and identification. He placed *Tylenchus* (= *Tylenchus*), *Cephalobus* and *Rhabditis* together because they had a striated cuticle, a ventral excretory gland and lacked a caudal sucker, but *Aphelenchus* was grouped with *Diplogaster*, *Plectus* and *Tripyla* because it had a sucker!

Otto Bütschli (1873, 1876) produced comprehensive illustrated descriptions of the free-living soil nematodes including several Tylenchida. In the words of Thorne (1961), 'Perhaps the credit for founding the science of nematology should belong to him, rather than to Bastian.' Örley (1880) published a system of classification for 202 nematode species in 27 genera and proposed the family Tylenchidae.

J.G. de Man produced excellent monographs on soil, plant and freshwater nematodes, which appeared in 1876, 1880, 1884 and 1921. His type specimens are deposited in the Zoological Museum of the University of Amsterdam, and these were restudied by Loof (1961). It is over 100 years since de Man (1884) first used the formula of  $\alpha$ ,  $\beta$ ,  $\gamma$  (now a, b, c) for measuring nematodes. The de Manian formula is universally used in the taxonomy of the Tylenchida today. de Man (1921) gave us the new tylenchid genera *Ecphyadophora*, *Hemicyclophora* and *Psilenchus*, and new species which later became types of new genera, namely, *Hoplolaimus annulifer* for *Nothocriconema* and *Tylenchus costatus* for *Coslenchus*.

I.N. Filipjev (1934, 1934a) based his system of classification on amphid shape, although he considered other characters as supplementary, i.e. he used a polythetic concept in classification. He underlined the importance of embryology and physiology in the relationships of nematodes with other groups – Acanthocephala, Echinodera, Gastrotricha, Gordiacea and Rotatoria. In 1934 he presented a comprehensive classification of the Class Nematoda, recognizing 11 orders: Chromadorata, Desmoscolecata, Enoplata and Monhysterata for free-living forms; Anguillulata for partly free-living, partly parasitic forms; Ascaridata, Dioctophymata, Filariata, Oxyurata, Spirurata and Trichurata for the animal-parasitic forms. Under Anguillulata, he recognized three families – Anguillulidae, Tylenchidae and Strongylidae – and under Tylenchidae he classified Tylenchinae, Hoplolaiminae, Sphaerulariinae, Diplogasterinae and Tylopharynginae by regarding the oesophagus with a median bulb as the unifying character of the group.

Filipjev (1934) argued that, in the plant-parasitic members of this group, the median bulb was the only muscular part of the oesophagus. It was reduced in males of certain species because they did not feed, and more so in Sphaerulariinae, in which the oesophagus and intestine did not function, as feeding was through the skin. He remarked that the Tylenchinae were characterized by a triple spear very like that of *Tylencholaimus* (Dorylaimida) but mostly with a strongly marked triple enlarged base. Hoplolaiminae with the criconematids were recognized as a highly specialized terrestrial group having cuticle with peculiar rings, sometimes subdivided to give a scale-like appearance and a peculiar, huge spear with basal knobs.

Filipjev (1934a) produced an important book on systematics in Russian, *Harmful and Useful Nematodes in Rural Economy*. In this work he assigned Tylenchidae, Anguillulidae and Strongylidae to the order Anguillulata. Within the Tylenchidae he recognized Tylenchinae, Hoplolaiminae, Sphaerulariinae, Diplogasterinae and

Tylopharynginae. Under Hoplolaiminae he considered the genera *Hoplolaimus*, *Atylenchus*, *Eutylenchus* and the criconematid genera *Criconema*, *Iota*, *Paratylenchus* and *Procriconema*. The criconematid genera *Hemicyclophora* and *Macroposthonia* were assigned to the Tylenchinae because they were based only on males lacking a stylet. *Dolichodorus* and *Nemonchus*, although having a large stylet, were also assigned to Tylenchinae, apparently because they had finer body annules than most Hoplolaiminae (*sensu* Filipjev). He proposed a new subgenus *Bitylenchus* under the genus *Tylenchus* and designated *Tylenchus dubius* Bütschli, 1873 as its type. He recognized five subgenera under *Tylenchus*, namely, *Anguillulina* (type indicated as *Vibrio tritici* Bauer, 1823 (= *Tylenchus tritici* auct.)), *Bitylenchus*, *Chitinotylenchus*, *Tylenchorhynchus* and *Tylenchus*, and gave a differentiating key. Filipjev's (1934a) book was later incorporated and enlarged into *A Manual of Agricultural Helminthology* by Filipjev & Schuurmans Stekhoven published in 1941. Filipjev did not see the publication or even its final version since his contact with Schuurmans Stekhoven was lost in 1937 and, according to Dr E.S. Kirjanova, Filipjev died on 22 October, 1940 (*vide* Mjuge, 1977).

In 1922 Heinrich Micoletzky of Austria produced a voluminous monograph *Die freilebenden Erd-Nematoden* listing 142 valid genera and 931 species of free-living (soil, freshwater and marine) and plant- and insect-parasitic nematodes under five families: Alaimidae, Odontopharyngidae, Rhabditidae, Trilobidae and Tylenchidae. To the family Tylenchidae, Micoletzky assigned Diphtherophorinae, Dorylaiminae and Tylenchinae, members of which are now placed under three different orders, Triplonchida, Dorylaimida and Tylenchida. In the subfamily Tylenchinae, he placed the following genera: *Tylenchus* (with *Chitinotylenchus* n.subgen.), *Allantonema*, *Aphelenchus* (with *Paraphelenchus* n.subgen.), *Dolichodorus*, *Eutylenchus*, *Heterodera*, *Hoplolaimus* (syn. *Criconema*, *Iota*), *Nemonchus*, *Parasitylenchus* n.g., *Paratylenchus* n.g., *Triplonchium*, *Tylenchorhynchus* and *Tylenchulus*. Although his familial groups were heterogeneous and his classification did not go beyond the family level, he did publish genealogical tables and family trees. Micoletzky was a 'lumper' for he believed that species varied greatly. He grouped diversified species under one genus and synonymized several otherwise valid species. In the words of Thorne (1961), 'He lumped together all species which were in any way similar to each other and thus produced an impossible conglomeration of trinomial nomenclature which other workers refused to accept.' But Micoletzky was a dedicated scientist with keen powers of observation and his monograph is a landmark in the history of nematology. He prepared excellent slides of nematodes, most of which are in excellent condition today in the Zoological Museum of the Humboldt University in Berlin, where the writer had the opportunity of studying them in 1975. The science of nematology is indebted to Micoletzky for making those long-lasting permanent slides by using dehydrated glycerine, and to an unknown person for their safety during World War II, who 'dumped' the slides, properly wrapped up in a bag, at the Zoological Museum of Berlin. The bag, lying in a corner, was discovered by Dr G. Hartwich (personal communication), who has looked after them ever since.

Baylis and Daubney (1926), in their synopsis of the families and genera of Nematoda, criticized Micoletzky's division of Tylenchidae into Diphtherophorinae, Dorylaiminae and Tylenchinae because the subfamilies were chiefly based on the stylet structure. These authors remarked that the system 'does not, however, appear

to us to offer a natural classification of the group, and it seems to us that a somewhat more satisfactory subdivision is arrived at by considering primarily the characters of the oesophagus'. Consequently, they proposed that Anguillulidae (their equivalent of Tylenchidae) should contain only Anguillulinae and Dorylaiminae! They placed Anguillulinidae under the order Ascaroidea (suffix -oidea was being used for ordinal rank at that time) and listed the following genera under Anguillulinidae: *Anguillulina*, *Aphelenchus*, *Heterodera*, *Hoplolaimus*, *Isonchus*, *Nemonchus*, *Psilenchus*, *Tylopharynx* and *Tylenchulus*; *Aphelenchoides* was listed under genera incerta sedis and *Myenchus* and *Myoryctes* were included in an appendix to the Anguillulinidae with a note that the genera were probably considerably modified due to their parasitic habits, but the presence of a buccal stylet showed their affinity to the members of the Anguillulinae. Baylis & Daubney took a drastic step in proposing the following genera as synonyms of *Anguillulina*: *Anguina*, *Aphelenchulus*, *Atylenchus*, *Chitinotylenchus*, *Dolichodorus*, *Eutylenchus*, *Iotonchium*, *Parasitylenchus*, *Paratylenchus*, *Tylenchorhynchus*, *Tylelenchus* and *Tylenchus*. T. Goodey (1932) proposed a large number of new combinations with *Anguillulina* because he thought *Tylenchus* was a synonym of *Anguillulina*.

The inclusion of free-living and animal-parasitic nematodes in a combined classification was done by Wülker (1924), who believed (see Wülker, 1929) that Ascaroidea were direct descendants of free-living marine forms.

Cobb's (1893) monograph, *Nematodes, mostly Australian and Fijian* contained several tylenchid nematodes, including *Radopholus similis*, which he proposed on the basis of the male as *Tylenchus similis*. The female of this species was described by him in the same paper as another species, *Tylenchus granulosus*. In 1913, he published *New Nematode Genera Found Inhabiting Freshwater and Non-brackish Soils* and in 1920, *One Hundred New Nemas (Type Species of 100 New Genera)*. His collected papers, *Contributions to a Science of Nematology*, is a valuable book containing articles on marine, soil, fresh-water, plant and insect nematodes with excellent illustrations made by W.E. Chambers. Cobb's (1920) system of classification of higher categories of nematodes based on the monothetic concept using the shape and structure of the stoma was never recognized. On this character, two subphyla were proposed by him – Laimia and Alaimia. Laimia was divided into two classes – Onchia and Anonchia, the former having onchia, teeth and/or the stylet, and the latter lacking them. Onchia, had two subclasses – Heteronchia with orders Axonchia and Anaxonchia, and Homonchia with orders Aponchia, Mesonchia, Synonchia and Triplonchia. Each of these categories became an assemblage of unrelated forms and the entire system proved artificial.

In 1919, Cobb proposed the Phylum Nemata and in 1932 gave it a diagnosis. Chitwood (1957) commented on its validity thus: 'The fact that Potts (1932) and the writer [Chitwood] in 1950 did not recognize Nemata Cobb, 1919, but rather synonymized it with the Nematoda (as a phylum) is lamentable. We can only say that the writer was young, foolish, and ignorant and did not realize the far-reaching importance and soundness of Cobb's work.' Such words of humility can only be expressed by one who is a really great person, as Chitwood undoubtedly was. His joint contribution with his wife, M.B. Chitwood, *An Introduction to Nematology*, is a milestone in the history of nematology. His work was mainly on the morphology and taxonomy of human, animal and marine nematodes, but in Tylenchida his contribu-

tions on *Meloidogyne*, *Hemicriconemoides* and *Criconema* and his new suborder Tylenchina had made him a 'plant nematologist'. Chitwood & Chitwood (1937) had considered the superfamily Tylenchoidea as a member of the suborder Rhabditina, and recognized three families – Tylenchidae (with Tylenchinae, Criconematinae and Hoplolaiminae), Allantonematidae (with Allantonematinae and Sphaerulariinae) and Myenchidae – under it.

After Cobb's death in 1932, Gotthold Steiner (8 April, 1886–21 August, 1961) became the leading nematologist in the USA. Steiner's (1949) publication *Plant Nematodes the Grower Should Know* not only introduced nematodes to the growers but did much to promote applied nematology. Similarly, T. Goodey's (1933) book *Plant Parasitic Nematodes and the Diseases They Cause* aroused great interest in the study of plant nematodes. In 1951, T. Goodey wrote the text *Soil and Freshwater Nematodes*, which was rewritten and enlarged by his son, J. Basil Goodey, and was published in 1963.

In the second half of the 20th century, nematology grew up fast and became a fully-fledged discipline of science with its own techniques, fields of research, textbooks and academic programmes. Although large-sized publications with 100 new species, such as those of Bastian (1865) and Cobb (1920), are relics of the past, present Tylenchida taxonomists have produced quite large publications with descriptions of numerous new taxa (Andrássy, 1954, 1979; Allen, 1955; Thorne, 1955; Das, 1960; Siddiqi, 1961, 1979a, 1980b; Sher, 1966, 1968; Thorne and Malek, 1968; Whitehead, 1968; Khan *et al.*, 1976, etc.). Several books and monographs dealing with Tylenchida have been published, namely, by Wachek (1955), Rühm (1956), Meyl (1961), Thorne and Malek (1961, 1968), Paramonov (1962, 1968, 1970), Decker (1969), Kirjanova & Krall (1969), Heyns (1971), Andrássy (1976), Dropkin (1980), Maggenti (1981), Siddiqi (1986), Bongers (1988), Ebsary (1991) and Dasgupta (1998) and those edited by Zuckerman *et al.* (2 volumes, 1971), Southey (1978), Zuckerman & Rohde (1981), Nickle & Welch (1984) and Nickle (1991). Checklists by Baker (1962) and Tarjan & Hopper (1974), pictorial keys to genera by Mai & Lyon (1975) and Mai & Mullin (1996) and *CIH Descriptions of Plant-parasitic Nematodes* edited by Willmott, Gooch, Siddiqi and Franklin are useful aids for taxonomic and identification work. At present, classification and phylogenetic relationships are being given due consideration, while new species and genera continue to be described increasingly. However, we are only part of the way in achieving a stable classification of Tylenchida. The effort which has begun must be sustained so that a more orderly basis for nematology can be provided.

Andrássy (1999) states that the total number of genera of free-living nematodes at present is 1940 (1788 established as genera, 152 as subgenera). Of these, 650 are in Torquentia, 570 in Secernentia (includes Tylenchida) and 705 in Penetrantia (plus 15 which are of uncertain position). Among free-living Secernentia, rhabditids comprise 241 and tylenchids (including aphelenchs) 329 genera, representing, respectively, 12% and 17% of all the free-living genera of nematodes. Andrássy (1999) lists the eight authors who have proposed more than 60 genera each, given here in alphabetical order in Table 1.

**Table 1.** Leading proposers of genera of free-living nematodes.

Author	Torquentia	Secernentia	Penetrantia
Allgén (1929–1959)	51	1	12 (+5 incerta)
Andrássy (from 1954)	10	47	67
Cobb (1891–1933)	127	21	60
Filipjev (1916–1946)	30	5	28
Jairajpuri (from 1964)	0	13	67
de Man (1876–1922)	32	8	21
Siddiqi (from 1959)	0	52	64
Thorne (1929–1974)	0	22	46

Source: Andrássy (1999).

## 4. TECHNIQUES

For identification and taxonomic study, good, clean specimens showing most anatomical details are essential. The proper killing and fixing of nematodes are the most important steps in obtaining good results. Permanent mounts are essential for long-term preservation. Details on the extraction, killing, fixing and mounting procedures of specimens are given by several authors (Oostenbrink, 1960; Thorne, 1961; Hooper, 1969; Southey, 1970; Taylor, 1971; Ayoub, 1977).

### Collection and Storage

Soil from the rhizosphere is collected after removing the top 3–5 cm of soil and litter layer. Soil and fine feeder roots are collected ideally in polythene bags which are then tied up and tagged with a label bearing details of the habitat, host, locality and other data such as soil type, associated vegetation and date of collection. To obtain interesting and new species, one should not forget to include rhizospheres of weeds, indigenous plants, grasslands, bushes and forest flora. Macrofungi, beetle frass, mosses and lichens can all harbour interesting Tylenchida fauna, especially that of Anguinoidea and Tylenchoidea, and should therefore also be examined. The samples should be processed as soon as possible, but if necessary they can be stored in polythene bags at about 4°C.

### Extraction

A number of methods exist for the extraction of nematodes. The choice of method depends on various factors, e.g. nematode activity (wet-funnel methods and use of filters), specific weight (flotation, elutriation, centrifugation and decanting techniques) and ultimately convenience. Plant tissues, fungi, mosses and lichens can be macerated and immersed in water. A food blender is useful for speeding the process up. The water is sieved after 24 h and the nematodes are then concentrated and collected. Insects and mites should be dissected in Ringer's solution or 1% NaCl to avoid the rupturing of nematode bodies that may occur in pure water.

Baermann's (1917) funnel technique is a primitive way of isolating nematodes from soil and plant tissues and should not be used in its original form, as it offers a recovery of less than 20% of other methods (Oostenbrink, 1970). Baermann's method has been modified in many ways, e.g. by Esser (1957) and Whitehead &

Hemming (1965). The Whitehead & Hemming method involves the use of large trays upon which a wire or plastic mesh supports a piece of tissue paper (such as Kleenex). The soil or plant material is thinly spread over the tissue, and the water is added so that the material on the tissue is just submerged. The active nematodes make their way through the tissue and collect at the bottom within 24 h. The water suspension is then concentrated by Cobb's (1918) sifting and gravity method. This method is good for motile nematodes but unsatisfactory for less active (such as criconematids) or inactive nematodes which are unable to pass through the tissue paper. The procedure should be carried out in a cool environment to avoid bacterial growth and hence depletion of oxygen and the trays should not be over-saturated with water.

The 'bucket-sieving' method described below, although crude, is widely used as it enables the extraction of a large number of both active and inactive nematodes in a relatively short time. About 300 ml of soil (more if sandy) is put in a bucket containing water. The mixture is vigorously stirred to give a suspension which is allowed to settle for a couple of minutes. The floating debris is removed by a very coarse sieve. The remaining suspension is slowly poured over a fine mesh sieve with 45–53  $\mu\text{m}$  aperture which is continuously tapped by hand to avoid blocking. The deposit on the sieve is washed with a very gentle jet of water into a beaker and this can be examined directly or further processed using a miniature version of the above Whitehead & Hemming tray method.

The centrifugal sugar-flotation technique of Caveness & Jensen (1955) is good for quick separation of nematodes (both motile and inactive) from the debris in a suspension. The sugar solution is prepared by dissolving 454 or 484 g of sucrose in 1 litre of water to give a solution of specific gravity 1.13 or 1.14. A 4–5 min spin at about 1750 rpm gives a satisfactory result. After spinning, the syrup containing nematodes is poured onto a fine mesh sieve and the nematodes are washed off into a dish for examination. To avoid the cost of sucrose, Rodriguez-Kábana & King (1975) advocate the use of molasses solution of sp.gr. 1–1.1 at 27°C which, due to its higher viscosity, gives a better recovery of nematodes than the sucrose solution.

An apparatus which uses a controlled water current passing through a sintered plate to separate nematodes from soil particles was described by Trudgill *et al.* (1973). Nematodes of all types and sizes can be extracted using this fluidizing column. Cyst nematodes can be isolated by this method. The Erlenmeyer flask method for isolating cyst nematodes from air-dried soils involves the differential sedimentation of nematodes and soil particles. The soil sample is placed in a conical flask and shaken with water. The cysts float and come to lie at the top within 15 min. The supernatant is poured onto a 100  $\mu\text{m}$  aperture sieve and washed. The debris containing the cysts is then poured off onto a filter paper held in a wide funnel and the cysts are picked individually off the paper under a dissecting microscope. There is no universal method for the quantitative extraction of all nematodes, the final choice being a personal one.

After comparing results of two centrifugal flotation techniques (direct centrifugation and sieving-centrifugation) with Seinhorst elutriation (1956, 1962a), Dunn (1971) recommends direct centrifugation as the least laborious and time-consuming. This involves placing about 50 ml of soil directly into a 250 ml centrifuge bottle, shaking vigorously with 200 ml of water and centrifuging for about 4 min at 1280 g

(sufficient to allow soil particles larger than  $0.5\ \mu\text{m}$  to sediment). The supernatant is discarded and the pellet re-suspended in 200 ml of 1.1 M sucrose solution (500 g sucrose in 1 litre tap water). It is centrifuged again for 4 min at 1280 g and the nematodes in the supernatant solution are collected after passing them thrice through a 45–53  $\mu\text{m}$  aperture sieve.

For the extraction of plant and soil nematodes, Persmark *et al.* (1992) compared Seinhorst elutriation, Cobb's decanting and sieving, the Whitehead tray method and the centrifugal-flotation method using silica, sucrose and  $\text{MgSO}_4$ . Colloidal silica ('Ludox LS'), sucrose and  $\text{MgSO}_4$  solutions with a specific gravity of 1.16 were used. For centrifugation, 600 g soil was dispersed in 3000 ml water and from it a 500 ml aliquot was taken. Plant-parasitic nematodes were recovered in largest numbers with the elutriator and the three centrifugal-flotation methods, and the largest *Pratylenchus* specimens were recovered by the Whitehead tray method. Centrifugal flotation with silica was superior for the extraction of trichodorids.

After extraction, nematodes can be examined directly under the microscope and counted using Winslow's or Fenwick's multichamber counting slides or counting trays. There are various types of handling needles for nematodes. A small piece of hair, fixed to the tip of a long needle on a glass or wooden rod is sufficient and useful. If nematodes are to be kept permanently, they must first be killed, fixed and properly mounted.

## Killing, Fixing and Processing

For obtaining good specimens for taxonomic studies, the method of killing is most important and critical. Some nematologists kill their nematodes in water by the gradual application of heat, either placing the dish containing nematodes in a constant-temperature oven at 65 or 70°C or slowly heating the nematodes in water in a test tube or on a slide over a naked flame, avoiding over-heating. A better method is to kill nematodes by applying sudden heat, i.e. by pouring hot water (90–95°C) over them after removing almost all the water from the container. Seinhorst's (1966) method which gives excellent specimens, involves pouring hot (90–100°C) formaldehyde–acetic (FA) or formaldehyde–propionic (FP) acid solution (4:1, i.e. ten parts 40% formalin, one part acetic or propionic acid and 89 parts distilled water) over nematodes.

To avoid deterioration and distortion during mounting, the nematodes are fixed soon after killing. Nematodes are best fixed in FP 4:1 or FA 4:1. A 3–5% solution of formaldehyde is good for fixing and storing nematodes. Courtney *et al.* (1955) advocate TAF (triethanolamine 2 ml, (40%) formalin 7 ml and distilled water 91 ml), but nematodes should not be left in it for more than a year. Esser's (1973) 4-min killing and fixing device uses a timer-operated, calibrated hot-plate to heat nematodes in water in a watch glass to 35°C. Stained lactophenol is added immediately and the heat is continued for a further 2 min.

For entomoparasitic nematodes, killing is best done by adding hot (80°C) Ringer's solution to nematodes. Mendola blue and Nile blue A and New blue R are used for distinguishing dead from living nematodes (*vide* Shepherd, 1962; Ogiga & Estey, 1975). Nematode structures are stained by acid fuchsin, gold chloride, picric acid–iodine, etc. Secretions from amphids, phasmids and excretory pores were induced and stained when nematodes were incubated in 0.1% Coomassie brilliant



blue G-250, in 40% aqueous methanol containing 10% acetic acid on a slide sealed with nail polish or Zut (Premachandran *et al.*, 1988). Nematode structures can be stained by several biological dyes, viz. Coomassie brilliant blue R, Evans blue, naphthol blue black, azure blue, toluidine blue, methyl orange, carminic acid, iodine green, haematoxylin and rosaniline hydrochloride.

Lactophenol (Amann, 1896: lactic acid 20 ml; phenol 20 ml; glycerine 40 ml and distilled water 20 ml) is a good clearing agent and widely used to process nematodes to glycerine. Siddiqi (1964) described a quick method of processing dorylaimid nematodes to glycerine; the same can be used with some modification for tylenchids. Fixed nematodes are transferred to hot lactophenol and left in it until the liquid becomes thick and syrupy. They are then transferred to a warm mixture of 75% glycerine and 25% lactophenol and kept warm for 5 min. The nematodes are finally transferred to pure glycerine and mounted in the same medium. For tylenchid nematodes with a thick cuticle, it is important that the nematodes are properly stretched in hot lactophenol by increasing heat or time until they are fully stretched. It may be necessary to leave them in lactophenol or glycerine–lactophenol mixture for 1–2 h before transferring to pure glycerine. Glycerine should be dehydrated and contain traces of menthol or picric acid to prevent bacterial or fungal growth. For staining methods, lactophenol may be tinted with cotton blue, aniline blue or acid fuchsin (0.0025% solution; 0.01% solution for staining nematodes in roots).

Propionic acid/orcein has been used for staining nematode chromosomes. Grisi *et al.* (1995) prepared the stain by mixing 2 g of orcein and 100 ml of 45% propionic acid. The mixture was boiled for 1 h, cooled and filtered before use. Slides with excised gonads of *Globodera pallida* were stained for 3 h and then washed in 45% propionic acid, mounted and sealed with glyceel.

Processing to glycerine takes longer but specimens so prepared will keep for a very long time. Fixed nematodes are placed in 2 ml of a solution of 1.5% glycerine in distilled water, in a small watch glass. This is then put in a desiccator chamber at 25–30°C, for about 4 weeks or until the water has been fully absorbed. A drop of copper sulphate or thymol can be added to the solution before desiccation in order to prevent the growth of moulds (Thorne, 1961). In Seinhorst's (1962) method, fixed nematodes are placed in a small watch glass containing 0.5 ml of the following solution: 96% ethanol 20 ml, glycerine 1 ml, distilled water 79 ml. The watch glass is then placed on a tripod above a dish containing 96% ethanol (1/10 volume of vessel) in a closed glass vessel. It is left for about 12 h in an oven at 40°C, by which time the specimens should be in a mixture of glycerine with some ethanol. The dish is removed and filled with a solution of five parts glycerine and 95 parts of 96% ethanol and then placed in an oven at 40°C. The ethanol should evaporate within 4 h, after which the nematodes, now in pure glycerine, can be mounted. It is possible to process nematodes from fixative to a permanent mount in glycerine within 1 h using Baker's (1953) rapid method to glycerine. The method involves staining nematodes in lactophenol cotton blue and then processing through a series of solutions for about 10 min each while maintaining at about 55°C. The solutions contain glycerine in increasing concentrations (55% to 100%) and lactic acid, phenol, distilled water and 40% formalin in decreasing concentrations.

The nematodes are best mounted on thin glass slides using 19 mm diameter

cover slips. The nematode(s) are placed in the centre of the slide in a very small drop of mountant. Glass rods (three pieces from one glass fibre about as thick as the nematode) or beads are placed around the nematode(s). Paraffin wax of 60–65°C melting point is placed as three lumps around the drop, each lump about the size of the drop or a little larger, and the cover slip is placed on the wax lumps. The slide is then heated on a hot-plate or over a flame just enough to melt the wax, which spreads and fills the space between the slide and cover slip, holding the nematodes in mountant in the centre.

To prevent drying, it is necessary to seal glycerine + wax slides by glyceel, Zut or Corseal. Corseal can be prepared by dissolving 10 g of Thermocol, a waste packing material, in 15 ml of chloroform, to which 20 ml of butyl acetate, 2 ml of alcohol-soluble linseed oil and 1.5 g of any hard plastic waste is added (Sabir, 1997). Clear nail polish is recommended as a sealant when glyceel or Zut is not available. Esser (1974) uses Zut (glyceel) to provide support in place of glass rods, glass beads or wax. A small drop of mountant containing nematodes is ringed closely by Zut and then the cover slip is placed on top and, if necessary, the Zut can be allowed to dry out a bit to make it more viscous. Slides can be sealed finally by ringing the coverslip using Zut.

Esser (1988) described a simple method for the examination of the vulval cone of mature cysts of *Heterodera* spp. A block of 1.7% water agar measuring about 1.5 cm × 1.5 cm × 2 mm high is put on a slide. A small 1 mm deep cavity slightly less than the diameter of the cyst is made on the agar block with a fine needle. A cyst is gently pushed into the cavity with the anterior end down until the vulva region of the cyst is level with the agar surface. A small drop of water is added to a 15 mm cover slip which is inverted and dropped over the embedded cyst. The slide is ready for viewing the vulval cone structures.

Counting nematodes in a suspension was made easy by using a GOP-302 image analysis system, manufactured by Context Vision, Sweden. The automated computerized image analysis of digitized images is described by Been *et al.* (1996). For clearing adhering tissues, the perineal patterns of *Meloidogyne* are treated with 45% lactic acid.

## Monoxenic Cultures

Monoxenic cultures of Tylenchida provide large populations for studies on taxonomy, biology and host–parasite relationships. Bingefors & Bingefors (1976) have cultured *Ditylenchus dipsaci* on callus tissue for longer than 14 years without change in the nematode's host specificity or aggressivity, and have distributed nematodes from a 'nematode bank' for use in breeding resistant plants.

*Heterodera oryzae* is reared on rice roots cultured axenically in test tubes (Reversat, 1975). *Pratylenchus* and *Heterodera* spp. are easily cultured axenically on excised roots. Seeds are surface-sterilized in 1–1.5% sodium hypochlorite solution for 10 min, germinated under aseptic conditions on 1.5% water-agar in Petri dishes and incubated at 20–25°C. Upon germination, radicles are aseptically incised and transferred to Petri dishes containing sterile tap water (STW) agar medium. The nematodes are surface-sterilized in 50 ppm streptomycin sulphate in aqueous solution, washed in distilled water, and added to the Petri dishes with root radicles which are incubated at optimum temperature for host development (Lauritis *et al.*, 1982).

## Interference and Scanning Electron Microscopy

Interference microscopy utilizes polarizing beam splitters and interference of optical paths to give a sharper image, particularly of surface structures. Nomarski's interference unit is fitted to a compound microscope and is used in conjunction with bright-field microscopy. For the former more light is needed but, unlike bright-field microscopy, the image is soothing to the eyes.

Scanning electron microscopy (SEM) is used to study surface structures, excised stylets, spicules and other tissues. Nematodes with a thin cuticle require proper fixation and dehydration to avoid shrinkage. They are washed in phosphate buffer (pH 6.8–7.4), fixed in 3% glutaraldehyde and/or 1% osmium tetroxide, washed in distilled water and dehydrated in a gradual series from 10% to absolute ethanol. Raski *et al.* (1980) passed nematodes in absolute alcohol through a graded series from 30% of amyl acetate in alcohol to absolute amyl acetate. McClure & Stowell (1978) described a simple method of processing nematodes in nylon mesh chambers during fixation, dehydration and critical-point drying or impregnation with embedding resin. In absolute alcohol or amyl acetate the nematodes are critical-point dried by using liquid CO<sub>2</sub>. The dried nematodes are mounted on stubs after the surface is first coated with a thin layer of glue (e.g. pieces of transparent sellotape dissolved in benzene or chloroform). The stubs are sputter-coated with gold (400–750 Å) and examined under an electron microscope. Högger & Esty (1977) described a method of cryofracturing to expose internal structures of nematodes for use under the scanning electron microscope.

Lippens & Grootaert (1974) described a routine method for mounting nematodes in ERL, an epoxy resin with low viscosity and high refractive index for light or electron microscopy. Nematodes are fixed for 2 h in 4% paraldehyde in Sorensen buffer at 4°C, rinsed in buffer and then post-fixed in 1% osmic acid in buffer for 1–2 h. The nematodes are dehydrated in a gradual series of acetone solutions. From acetone they are transferred to a 1:4 mixture of ERL and acetone, left for 20 h and then transferred and kept in 100% ERL for 2 h. After mounting in ERL, they are kept for at least 24 h at 60°C. De Grisse (1974) and Clark & Stone (1975) used Spurr's low-viscosity epoxy resin to avoid tissue collapse and surface tension damage.

Abrantes & Santos (1989) described a method of preparing perineal patterns of *Meloidogyne* for SEM study. Females were placed in a large drop of 45% lactic acid on a plastic slide or slab and the perineal patterns were cut and cleaned. Up to ten patterns were then transferred to a small drop of 45% lactic acid on a cover slip rimmed with a thick ring of glyceel and oriented so that the surface side was facing up. The cover slip with the chamber containing patterns was placed on a glass slide and fixed by applying a drop of glyceel to the edge. One drop of 2% formalin was then added every 2–3 min to the chamber to wash out the lactic acid. After 10 min the formalin solution was absorbed by a filter paper and the patterns were allowed to dry in a desiccator at room temperature. The cover slip was then detached from the glass slide and mounted on an SEM stub with a double-sided adhesive tape, coated with 200 Å of gold, and examined with SEM.

Successful cryopreservation by freezing and storing in liquid nitrogen at –150 to –200°C of free-living and plant-parasitic nematodes is now possible. Cryopreservation of plant-parasitic nematodes is useful for long-term storage. Freezing and storing of *Ditylenchus dipsaci* in liquid nitrogen is described by Sayre &

Hwang (1975). Second-stage juveniles of *Meloidogyne graminicola* were successfully preserved in liquid nitrogen using ethanediol (ethylene glycol) as a cryoprotectant. Juveniles were first incubated in 10% (v/v) ethanediol at 37°C for 15 min and then in cold 40% ethanediol for 30–45 min before freezing in liquid nitrogen to –196°C. The recovered juveniles after thawing infected rice roots and multiplied, producing large populations of females and eggs after 40 days (Bridge & Page, 1986).

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# II Morphological Characters and Taxonomic Methods

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## 1. MORPHOLOGICAL CHARACTERS

Since the morphological characters are the basis for the differential diagnoses of the various genera and higher categories and since they will continue to be the basis for the identification and systematics, it is important to examine them in some detail and to remain aware of the developments that take place in the observation, identification and interpretation of these characters. Morpho-anatomical characters are studied by using LM (light microscope), SEM (scanning electron microscope) and TEM (transmission electron microscope). The present discussion on the morphology of Tylenchida should present the reader with a clearer picture and a more comprehensive account of the various symbols, measurement ratios, structures and structure states used in the diagnoses of, and keys to, the various taxa from the subgenus to the order.

### (i) Morphometry and Allometry

de Man (1884) proposed the following formula of body ratios for nematode measurements:

$$a = \frac{\text{body length}}{\text{maximum body width}}$$

$$b = \frac{\text{body length}}{\text{oesophageal length}}$$

$$c = \frac{\text{body length}}{\text{tail length}}$$

These ratios are widely used in the description of new species of Tylenchida today, although they vary greatly within species. Other ratios and symbols include the following:

$$V = \frac{\text{distance from head end to vulva}}{\text{body length}} \times 100$$

$$T = \frac{\text{distance from cloacal aperture to anterior end of testis}}{\text{body length}} \times 100$$

$$b' = \frac{\text{body length}}{\text{distance from head end to posterior end of oesophageal gland}}$$

$$c' = \frac{\text{tail length}}{\text{body width at anus}}$$

$$V' = \frac{\text{distance from head end to vulva}}{\text{distance from head end to anus}} \times 100$$

m = length of conus as percentage of total stylet length

O = distance between stylet base and orifice of dorsal oesophageal gland as percentage of stylet length

MB = distance between anterior end of body and centre of median oesophageal bulb as percentage of oesophageal length

R = total number of body annules

Roes = number of annules in oesophageal region

Rex = number of annules between anterior end of body and excretory pore

RV = number of annules between posterior end of body and vulva

RVan = number of annules between vulva and anus

Ran = number of annules on tail

VL/VB = distance between vulva and posterior end of body divided by body width at vulva

## (ii) Body Shape

All migratory Tylenchida are eel-like and vermiform. The body is elongate cylindrical, tapering towards the extremities. It is extremely slender in Ecphyadophoridae and due to the relatively thick transparent cuticle appears like a glass fibre. In juveniles and females of Criconematidae it is thick, sausage- or spindle-shaped. The body posture on death or in relaxed condition (= habitus) is used as a diagnostic character. Usually the habitus is straight to slightly arcuate ventrally, but spiral coiling is not uncommon. In some entomoparasitic groups (Contortylenchidae, *Spilotylenchus*) and in gall-inhabiting *Fergusobia* females and *Anguina* males, the body, especially the posterior region, is curved dorsally with the ventral side facing outermost.

The sedentary nematodes which feed at one site inciting nurse or transfer cells for a continuous supply of food (see Fig. 6), or which parasitize insect or mite haemocoels, have swollen or obese bodies. The obesity of root-parasitic females is apparent in several groups (Meloidogynidae, Heteroderidae, Paratylenchidae, Sphaeronematidae, etc.). It cannot be the sole character for classifying them together. The female obesity has necessitated various modifications in the males (reduced tail, loss of bursa). The proposal of Heteroderoidea, as against Hoplolaimoidea, was mainly on the characters which relate to such functional adaptations and hence are not acceptable as valid.

### (iii) Body Symmetry

Nematodes are bilaterally symmetrical except in the anterior region where a radial symmetry is seen. However, the radial symmetry of the anterior end can be interpreted as a manifestation of the bilateral symmetry, e.g. the hexaradiate cephalic framework has one dorsal and one ventral arm and two arms on either side of the dorso-ventral plane.

In a bilaterally symmetrical body, a dorso-ventral longitudinal split would produce two similar halves. The oral aperture is terminal, the excretory pore, vulva and anus lie on the midventral line, while the amphids, deirids and phasmids lie on the midlateral lines (except prophasms in the Tylenchidae which are dorso-sublateral). The body can be divided into four equal **quadrants** delimited by latero-dorsal and latero-ventral radii, i.e. one dorsal, one ventral and two laterals. If each quadrant is further divided into two equal halves by the medio-dorsal, medio-ventral or medio-lateral radius, eight **octants** are obtained – two subdorsal, two subventral and four sublaterals.

The radial symmetry is seen in the oesophagus (e.g. muscular median bulb and glandular basal bulb). In the oesophagus there are one dorsal and two ventro-sublateral sectors delimited by the two dorso-sublateral and one medio-ventral radii (see Coomans, 1979). The dorsal and subventral oesophageal glands are symmetrically placed in these three sectors in the basal bulb of most Tylenchidae. But in spite of their ventro-sublateral position, the paired oesophageal glands are here called subventral glands.

### (iv) Body-wall

The body-wall consists of the external cuticle, hypodermis and somatic muscle layer. It forms a tube that encloses tubular digestive and reproductive organ systems. The muscle layer is composed of longitudinal muscle cells and the cuticle layer is such that it allows the body to expand much more lengthways than circumferentially.

The **cuticle** is the exoskeleton of nematodes. It is a non-cellular proteinaceous secretion of the hypodermis (= epidermis) and covers the entire body, intruding to line the stoma, oesophagus, excretory duct, vagina, rectum and cloaca. The protrusible stylet and spicules are of cuticular origin. The external cuticle may be secondarily lost in some females parasitizing insect and mite haemocoels that absorb food through the general body surface. The cuticular markings and modifications provide important morphological diagnostic characters.

The body cuticle of *Hirschmanniella* spp. consists of six layers (as does that of *Bitylenchus dubius* according to Byers & Anderson, 1971) divisible into three zones – an outer trilaminar **cortex** (epicuticle), a two-layered **matrix** (exocuticle) and a striated **basal layer** (? infracuticle) – as shown by Johnson *et al.* (1970). The body covering of female *Hemicycliophora arenaria* comprises a body cuticle and a cuticular sheath. The body cuticle is five-layered and also has three zones (cortex, matrix and basal layer) while the sheath is seven-layered. The male of this species has a six-layered body cuticle in three zones, and a thin outermost four-layered sheath (Johnson *et al.*, 1970). The cuticle of *Macroposthonia xenoplax* has three zones – cortex, matrix and striated zone (De Grisse, 1972a).

Mounport *et al.* (1993) found the ultrastructure of the cuticle of Hoplolaiminae to be different from that of members of the Anguinidae, Pratylenchidae,

Telotylenchinae and Heteroderidae. They reported a six- to seven-layered cuticle in Hoplolaiminae as compared to three-layered in Anguinidae, four-layered in Pratylenchidae or Telotylenchinae and four- or five-layered in Heteroderidae. Within the Hoplolaiminae, three groups could be identified depending on the ultrastructure of the cuticle and thickness of the basal layer: (i) *Hoplolaimus*, *Aorolaimus*, *Scutellonema* spp. with a seven-layered cuticle, lateral-field incisures not deep and a basal layer with thick fibres representing one-half of the cuticle thickness; (ii) *Aphasmatylenchus* and *Rotylenchus* spp. with a six-layered cuticle, lateral fields with deep longitudinal incisures and a basal layer with thick fibres representing one-half of the cuticle thickness; and (iii) *Helicotylenchus* and *Pararotylenchus* spp. with a six-layered cuticle, lateral fields with deep longitudinal incisures in *Helicotylenchus* sp. and a basal layer with thin fibres representing less than a quarter of the cuticle thickness.

The cuticle in Heteroderidae is four- or five-layered and is used in generic identification. The outermost **epicuticle** and **exocuticle** constitute the so-called **A layer**, and the **endocuticle**, which is striated and demarcated by a basal boundary, is named the **B layer**. Male and second-stage juveniles have only A and B layers, but the females of *Heterodera* and *Punctodera* have an additional **C layer** and *Globodera* and some other genera have a further **D layer**, which is important in differentiating between genera (Baldwin and Mundo-Ocampo, 1991; Zunke and Eisenback, 1998).

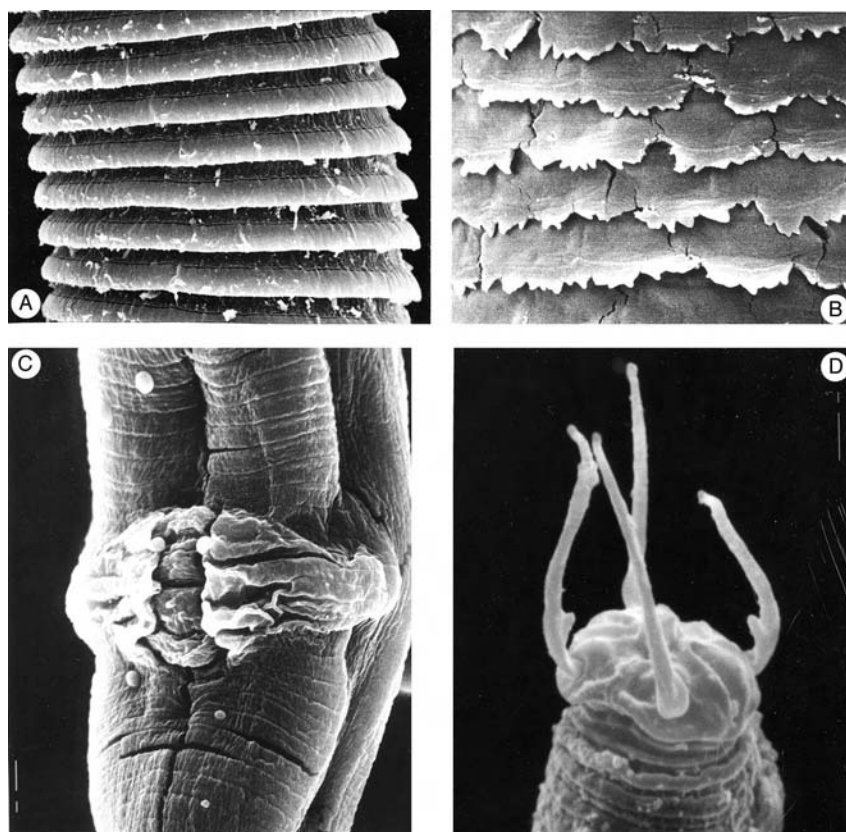
Maggenti (1979) and Siddiqi (1980) pointed out the phylogenetic significance of the cuticular strata. Maggenti (1979, 1981) stated that many Diplogasteria, including Tylenchida and Aphelenchida, have a cuticle consisting of epicuticle and exocuticle only as compared with the Spiruria, which have a third layer, the **meso-cuticle**, and with most Enoplia, which have a further additional layer, the endocuticle. The occurrence of epicuticle and exocuticle only in *Panagrolaimus* (Cephalobida) led Siddiqi (1980) to postulate that Tylenchida are probably more closely related to Cephalobida than to Rhabditida, Strongylida, Ascaridida and Spirurida.

Cuticular modifications (annules, scales, spines, sheath, etc.) and thickness (general as well as localized) are widely used in diagnostic differentiation of tylenchid genera in this work. The retrorse annules found only in Criconematoidea are special adaptations of this group and the cuticular scales and spines occur only on such retrorse annules (Fig. 8(a)A & B). The thick cuticle of retrorse annules helps criconematids to crawl along like earthworms, with the body kept straight. The nature and structure of the cuticular sheath of juveniles of Hemicycliophoridae are unique not only in the Tylenchida, but also in the entire Phylum Nematoda.

The **hypodermis** (= epidermis) lying beneath the cuticle is a cellular or syncytial layer being very thick at the **chords** (two laterals, one middorsal and one mid-ventral). The interchordal layers contain several **hemidesmosomes** (special sites of adhesion) which are particularly numerous where muscles attach to the body-wall (Byers & Anderson, 1971). The chords contain nuclei, mitochondria, endoplasmic reticulum and other cell bodies.

The **somatic muscles** are elongate-spindle-shaped cells beneath the hypodermis and attached to it. They are arranged longitudinally in the body and often form four groups being separated by the four hypodermal chords. The dorsal and ventral body muscles contract not in phase but in alternate rhythm resulting in a sinusoidal locomotory wave. A slow version of this rhythm also helps in gut and egg movement





**Fig. 8(a).** Scanning electron micrographs of cuticular structures. A. *Macroposthonia pruni* (Siddiqi), female from India: retrorse annules at midbody. B. *Blandicephalanema* sp. female from New Zealand: retrorse annules with dentate scales at midbody. C. *Pterotylenchus cecidogenus* Siddiqi & Lenné, paratype female from stem-gall of *Desmodium ovalifolium* from Colombia: lateral vulva membranes partially covering the vulva. D. *Eutylenchus africanus* Sher, Corbett & Colbran, female from coconut soil in Kerala, India: head and cephalic setae.

down the passageway. In *Criconemoides* the somatic muscle cells are basically **platymyarian-meromyarian** and contain several myofibrils and are obliquely striated (Bird, 1970). Many somatic muscles become specialized to perform certain functions, e.g. protractors and retractors of spicule, gubernacular and vulval muscles.

### (v) Lateral Field

Laterally, the body cuticle is generally marked by longitudinal incisures (lines, involutions; these are longitudinal invaginations of the external layer of the cuticle) and may or may not be raised into longitudinal **ridges** or bands, often interrupting the transverse body striation or annulation. The field originates as a narrow area or ridge and gradually enlarges to become of normal width behind the oesophagus and finally to end near the tail tip. The number of longitudinal lines or **incisures**

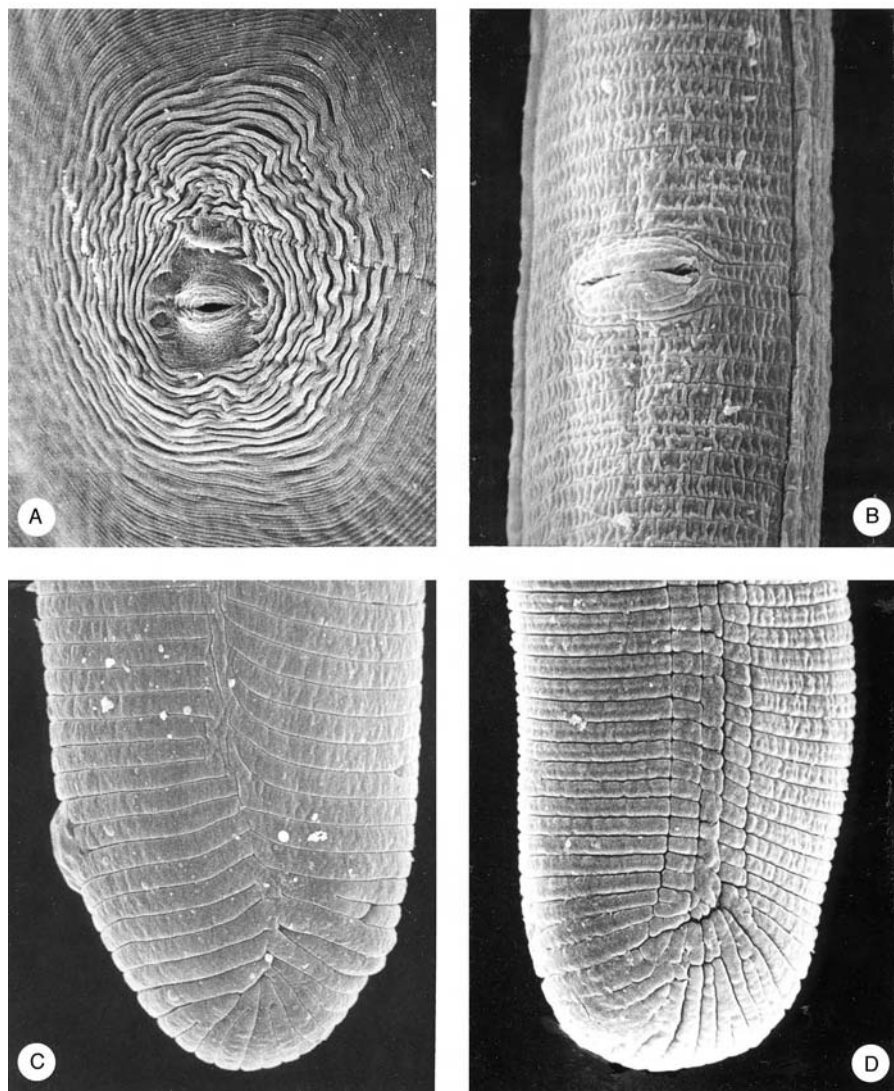
decreases towards the extremities, so that in descriptions the number taken at about the middle of the body is used. This is important because in certain cases, e.g. *Cephalenchus* spp., there are six incisures in the prevulval, but only four in the postvulval region, and the genus was differentiated from *Imphalenchus* which has only four incisures along most of its body. Mostly the fields have plain longitudinal bands (ridges) interrupting the transverse striations. If the transverse striae extend into the lateral field, the latter is known as areolated (or inappropriately aerolated).

If there is a single ridge (e.g. Duosulciinae) the outer margins of the ridge appear as two incisures. Two ridges may appear as three incisures when they are close together, or as four incisures when they are separated by a depression or gap (e.g. some *Coslenchus* spp.). The lateral field of *Cephalenchus* has six incisures and shows five distinct ridges (see Fig. 8(c)B). The single ridge of *Malenchus* is marked by numerous fine longitudinal lines. Hence it is important to differentiate between longitudinal lines and ridges. The ridges of the lateral field may be absent, but the incisures in such cases may be present (e.g. *Hoplolaimus* spp.) or absent (e.g. *Basirolaimus* spp.) (see Fig. 8(b)). Sometimes the lateral field is a simple groove (*Belonolaimus*, some *Hemicyclophora* spp.) or a zig-zag line (criconematids). The lateral fields may be lacking, as in Criconematidae juveniles and females and obese females of some genera (*Heterodera*, *Sphaeronema*). *Anguina* spp. and *Aphelenchulus mollis* may have 12 or more incisures in the lateral fields, but generally two to six incisures is the norm within the Tylenchida. Longitudinal ridges outside the lateral fields may also occur (see Fig. 8(c)). The lateral-field ridges are usually different from other longitudinal body ridges (*Coslenchus*, *Eutylenchus*, *Atylenchus*), but sometimes they cannot be distinguished from them (*Pleurotylenchus*, some *Neodolichorhynchus* spp.).

Lateral fields are useful taxonomic characters, e.g. Duosulciinae and *Quinisulcius* have been differentiated from Tylenchinae and *Tylenchorhynchus* respectively, primarily on the character of the lateral field (Siddiqi, 1971, 1979a). Merliniinae and Tyldorinae have members with six incisures in the lateral fields. However, the number of incisures may vary among generic groups and other supplementary differentiating characters must be found. *Imphalenchus* was made a junior synonym of *Cephalenchus* because no other supplementary character could be found.

## (vi) Excretory System

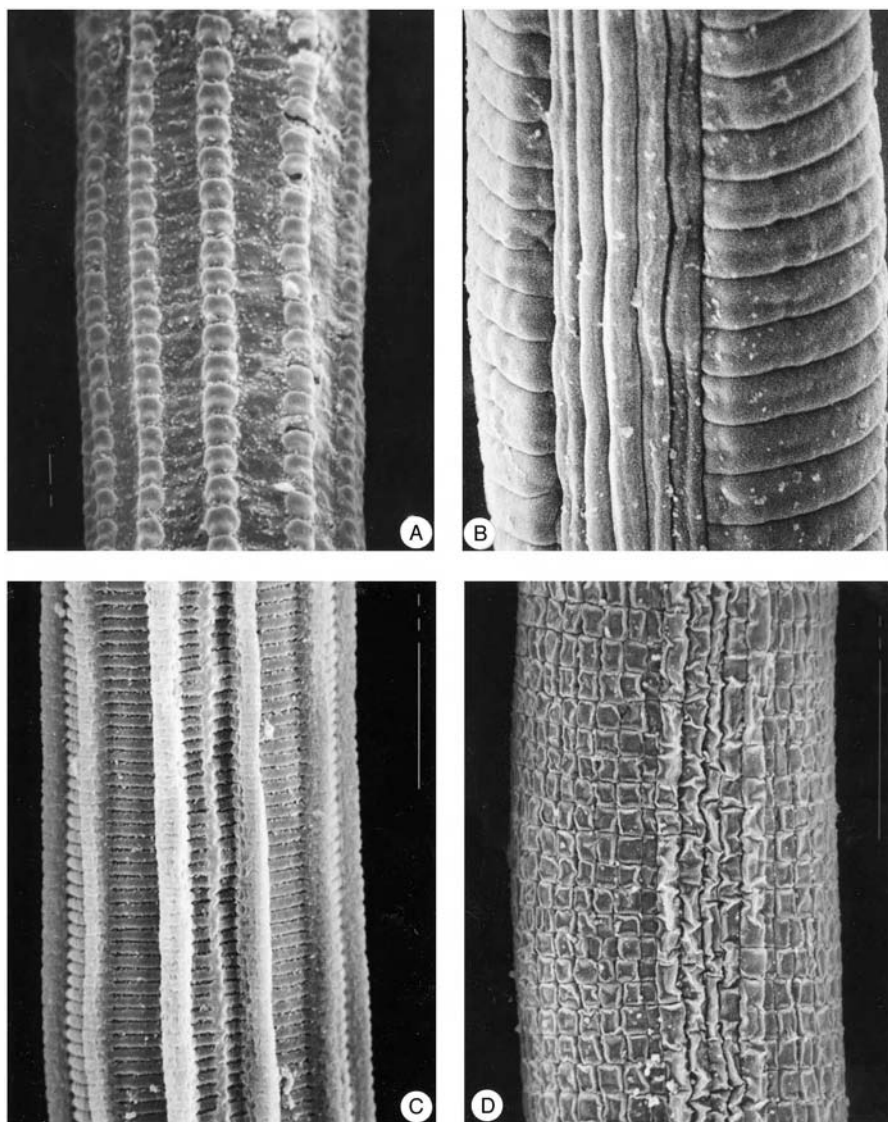
The excretory system (or excretory–secretory system) of Nematoda provides characters of taxonomic and systematic significance. In Tylenchida, the system is asymmetrical with a single excretory cell or renette situated laterally or latero-ventrally, generally in the post-oesophageal region, from which an excretory duct leads to the medio-ventral excretory pore. The renette may become exceedingly large to produce a sticky gelatinous matrix in which eggs are deposited (*Tylenchulus*). The excretory duct is lined with external cuticle, and occasionally it may be wide and sclerotized (*Halenchus*, *Allotylenchus*, *Neomisticus*). The excretory pore is generally located a little behind the level of the nerve ring, but may be close to the cephalic region (*Neomisticus*, *Kurochkinitylenchus*) or as far posterior as to lie close to the vulva (*Tylenchulus*). In Criconematoidea and Hemicyclophoroidea, the excretory pore is located at or behind the base of the oesophagus.



**Fig. 8(b).** Scanning electron micrographs of cuticular structures. A. Perineal pattern of *Meloidogyne incognita* (Kofoed & White). B. Vulval region in ventral view of *Zygotylenchus guevarai* (Tobar Jiménez). C. Lateral field on female tail end of *Hoplolaimus* (*Basirolaimus*) *indicus* (Sher). D. Lateral field on female tail end of *Hoplolaimus* (*Hoplolaimus*) *aorolaimoides* Siddiqi, paratype.

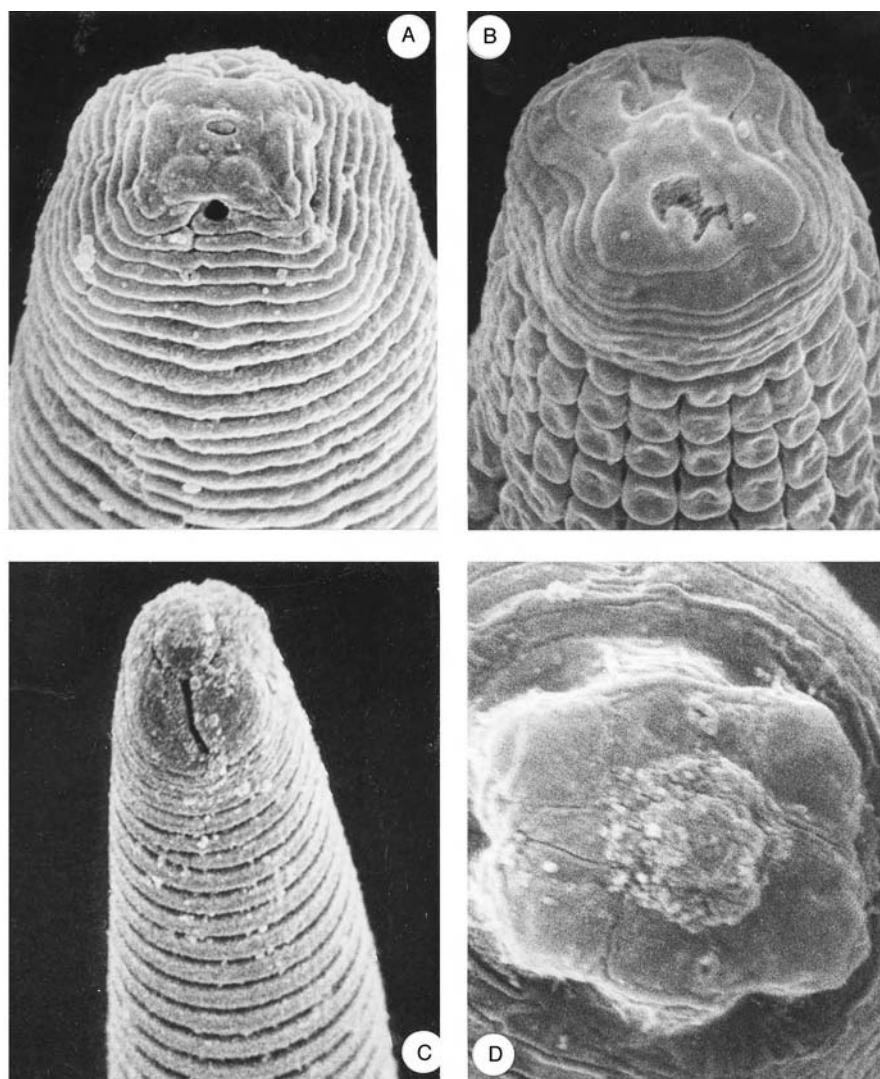
### (vii) Nerve Ring and Other Commissures and Sense Organs

The nerve ring encircles the isthmus of the oesophagus (circum-oesophageal ring) throughout the Tylenchida except in some Hexatyline (e.g. Neotylenchidae) where the nerve ring encircles the intestine lying behind the oesophago-intestinal junction



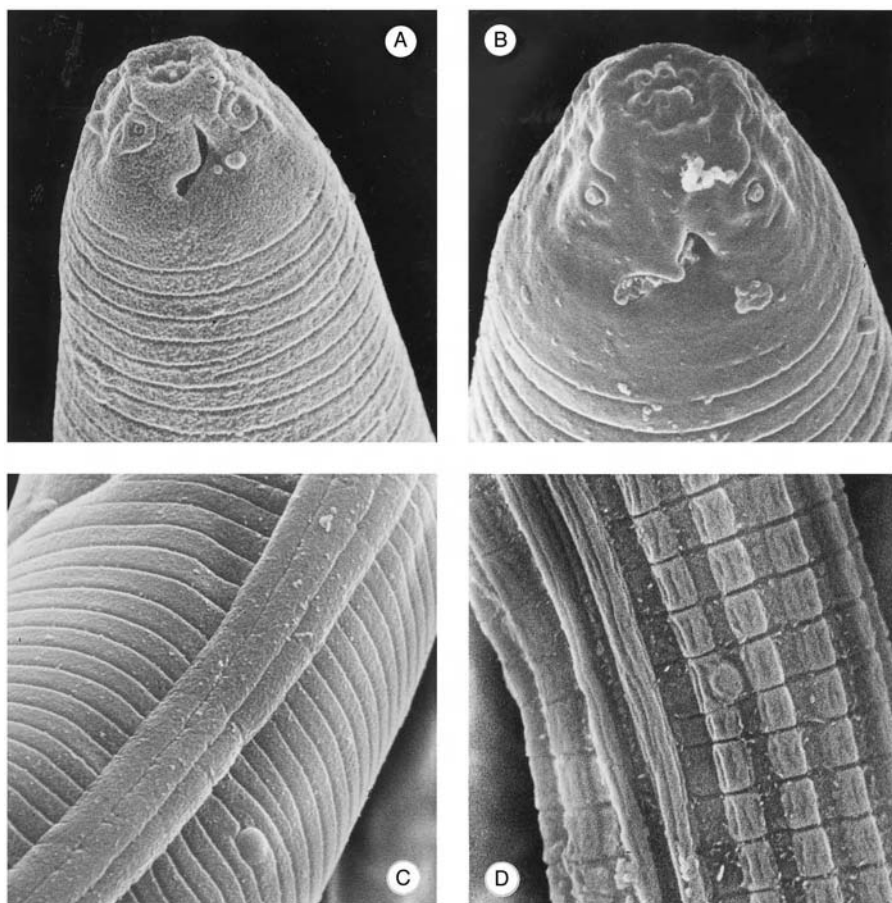
**Fig. 8(c).** Scanning electron micrographs of cuticular structures. A. *Eutylenchus africanus* Sher, Corbett & Colbran, female from coconut soil in Kerala, India, showing longitudinal cuticular ridges marked by transverse grooves. B. *Cephalenchus* sp. showing six incisures (five ridges) in lateral field. C. *Neodolichorhynchus* (*Mulkorhynchus*) *prophasmsis* (Jairajpuri & Hunt), paratype, showing longitudinal cuticular ridges. D. *Scutylenchus rugosus* (Siddiqi) from wheat soil in Afghanistan, showing lateral field with six incisures and longitudinal and transverse striae.

(circum-intestinal ring). From the nerve ring, nerves extend to the amphids and cephalic sensilla and backwards to the tail, one running through each of the four hypodermal chords, but the ventral nerve is more prominent. Several paired com-



**Fig. 8(d).** Scanning electron micrographs of head showing amphidial apertures. A. *Histotylenchus histoides* Siddiqi. B. *Coslenchus costatus* (de Man). C. *Tylodorus* sp. from *Eucalyptus* sp., Adelaide. D. *Fergusobia magna* Siddiqi from *Eucalyptus* shoot-gall in Brisbane, Australia.

missures connect these nerves and some laterolateral commissures can be seen in unstained nematodes. They have been given names and used in taxonomic descriptions and differentiations. The **hemizonid**, named by J.B. Goodey (1951), is the major latero-ventral commissure near the excretory pore. The **cephalids** (anterior ones just behind the cephalic region and posterior ones at some distance behind them) were named by Hirschmann (1956). The **hemizonion** occurring a little

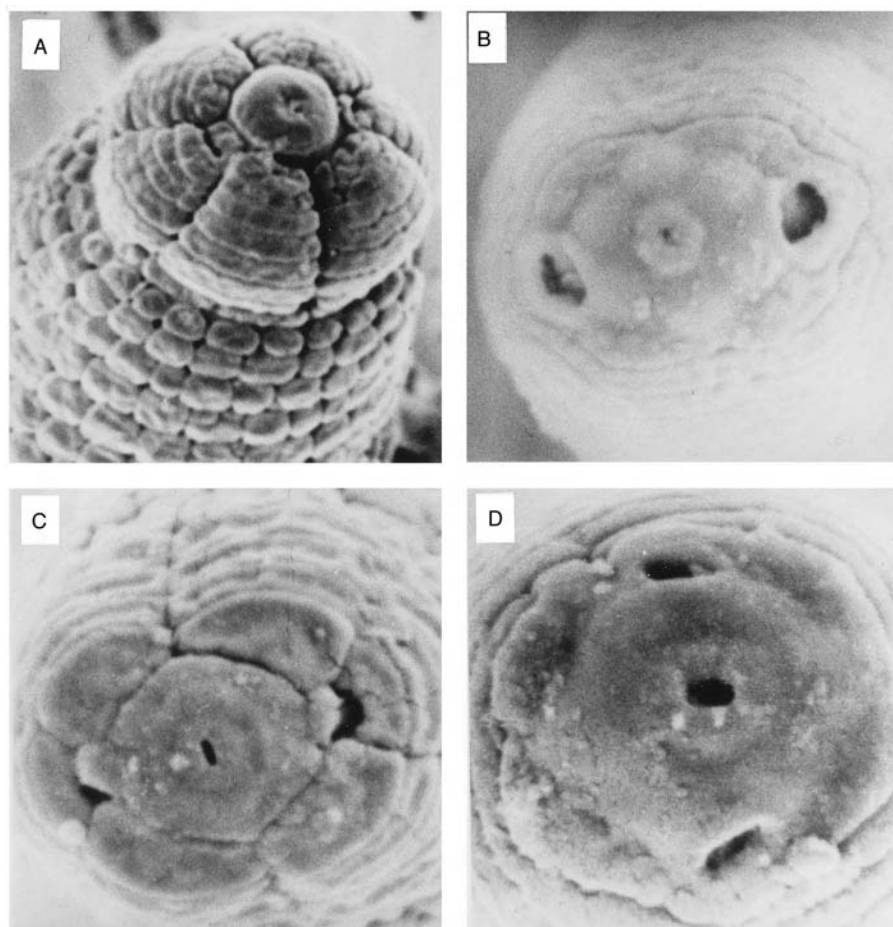


**Fig. 8 (e).** Scanning electron micrographs. A. *Boleodorus thylactus* Thorne, female head. B. *Neopsilenchus magnidens* (Thorne), female head. C. *Tylenchus davainei* Bastian, prophasmid dorsal to lateral field in vulval region. D. *Coslenchus costatus* (de Man ), prophasmid in vulval region. (A–D. After Brzeski & Sauer (1983), courtesy *Nematologica*.)

behind the hemizonid was named by Caveness (1961). **Caudalids** in the tail region were discovered by Rhode (1883) (see Chitwood, 1950) and correspond to the paired, ano-lumbar commissure linking the preanal ganglion to the lumbar ganglion.

### Cephalic sensory system

The cephalic sensory system of *Rotylenchus robustus* has 18 branches of six nerve trunks. The six labial nerves, each having two ciliary elements, open through pores (pits) in the vestibule (prestoma) and not on the surface of the labial disc. The lateral external labial nerves, each with a single ciliary process, are short, possibly due to the reduction of the lateral lip sectors and the relatively large size of the amphids; the other four submedian external labial nerves shift position with respect to the



**Fig. 8(f).** Scanning electron micrographs of female heads. A. *Geocenamus longus* (Wu, 1969). B. *Nagelus aberrans* Thorne & Malek, 1968. C. *Scutylenchus quadrifer* (Andrássy, 1954). D. *Amplimerlinius icarus* (Wallace & Greet, 1964). (Courtesy Rothamsted Experimental Station, Harpenden.)

four submedian cephalic nerves. External labial and cephalic nerves do not open or project like papillae externally but end blindly beneath the cuticle of the head (see Fig. 10A). The amphidial nerve contains 11 ciliary processes, seven of which are enclosed within the amphidial ampulla (cf. Fig. 9) (De Grisse *et al.*, 1974). The cephalic nerves project, in the form of setae, in members of the family Atylenchidae only (Fig. 8(a)D). A detailed review of the cephalic sensory system can be found in Coomans & De Grisse (1981).

### Amphids

These are a pair of lateral chemoreceptors located in the cephalic region, generally close to the oral aperture. In Hexatylna the amphidial apertures are minute pores

located dorso-sublaterally at some distance from the oral aperture near the level of the cephalic sensilla (Fig. 8(d)D). The amphid aperture may be slit-like, transversely, longitudinally or obliquely placed on the head (Fig. 8(d)); occasionally the slit may be long and sinuate (e.g. *Ecphyadophoroides*). In Criconematina the amphid apertures are close to the oral opening, facing forward. The amphid fovea (pouch) is greatly reduced in size. There are six to eight duct receptors and three to six sheath receptors with dendritic elements (see Fig. 9) (for details see Coomans & De Grisse, 1981).

### Deirids

In Tylenchidae and Merliniinae deirids are located in the centre of the lateral fields in the form of protuberances (cervical papillae) without an opening to the outside (Siddiqi, 1971; Brzeski & Sauer, 1983); a definite nerve appears to connect to each deirid. The deirids are common in Tylenchoidea and Hexatyulina lying at or near the level of the excretory pore. Among the Merliniinae, the genus *Scutylenchus* lacks deirids but other genera of this subfamily have distinct deirids.

### Phasmids and prophasms

Phasmids are chemoreceptors on the tail of the Hoplolaimina, but may also be located in the preanal region or erratically placed on the body. They are absent or have never been detected with certainty in Hexatyulina or Criconematina. In Hoplolaimina they occur in the middle of the lateral fields. Siddiqi (1978) found phasmid-like structures called prophasms, in Tylenchidae lying in the post-median region of the body, in females near the vulva – a discovery considered to be an epoch-making event! (I. Andr  ssy, F.G.W. Jones, *in litt.*). These prophasms have been the basis for recognizing Tylenchoidea as distinct from Hoplolaimoidea and Dolichodoroidea by Siddiqi (1986). Prophasms have also been found in Anguinidae by Sturhan & Rahi (1996).

The phasmids have a ciliary receptor and a nerve connection and open to the exterior through a small pore. The pore leads into a cuticle-lined duct which ends in a cell, the **socket cell**, which is possibly a modified hypodermal cell. There is an associated **sheath cell**. The phasmidial aperture may have a plug, possibly formed from polysaccharides secreted by the sheath cell. The plug may be small, as in Merliniinae, or large and scutellum-like, as in Hoplolaiminae.

### (viii) Cephalic Region

Cephalization or the possession of a head is suggested by the presence of a cuticular cephalic framework and the juxtaposition of the oral opening, sensilla and amphid apertures. The cephalic region (= lip region) may or may not be marked off from the body by a depression, constriction or expansion. The base of the cephalic region is the transverse line passing through the basal plate, although the outer and inner margins of the framework extend a few annules into the body from the basal plate.

Most Tylenchina and Hexatyulina have a small six-lobed or hexagonal cephalic region which may also be four-lobed, bilobed or rounded. *Belonolaimus* and *Dolichodorus* spp. have a four-lobed head with two large subdorsal and two large subventral lobes; lateral lobes are reduced. The head shape provides an important



diagnostic character for differentiation; Eisenback (1982) used it to distinguish between juveniles of *Meloidogyne* spp.

### Cephalic framework

The cephalic framework of Tylenchida is basically hexaradiate with one middorsal, one midventral, two subdorsal and two subventral arms or blades. There is a **basal plate** from which a tubular or inverted funnel-shaped **vestibulum extension** (= stylet-guiding apparatus) extends into the body cavity. The framework may be low arched (Anguinoidea, Pratylenchidae) or high arched (Hoplolaimidae, most Dolichodoridae). It is sclerotized to various degrees from light (Anguinidae) to heavy and yellowed (Hoplolaimidae). In Hexatylinea the framework may be six-, eight- or 12-sectored. *Hexatylus viviparus* has a framework six-sectored near the base and 12-sectored anteriorly. Some of the protractor muscles pass through the sectors to attach to the base of the external cuticle at the top of the head.

The cephalic framework of *Bitylenchus dubius* has a central (axial) tube of electron-dense cuticle and six radiating arms of less electron-dense cuticle. The oral opening leads into the prestoma that opens into the vestibulum or the central tube. The vestibulum extension projects into the body cavity, its cuticle attaching to the stylet shaft (Byers & Anderson, 1971).

### Stoma

The stoma or stomatal cavity is lined with an external cuticle and extends from the anterior end of the body to the base of the stylet conus. In several groups (e.g. Hoplolaimidae, Criconematidae) the inner labial sensilla are situated inside the stomatal cavity and indicate an invagination of the lip areas and hence the anterior-most region of the stoma is called the **prestoma**.

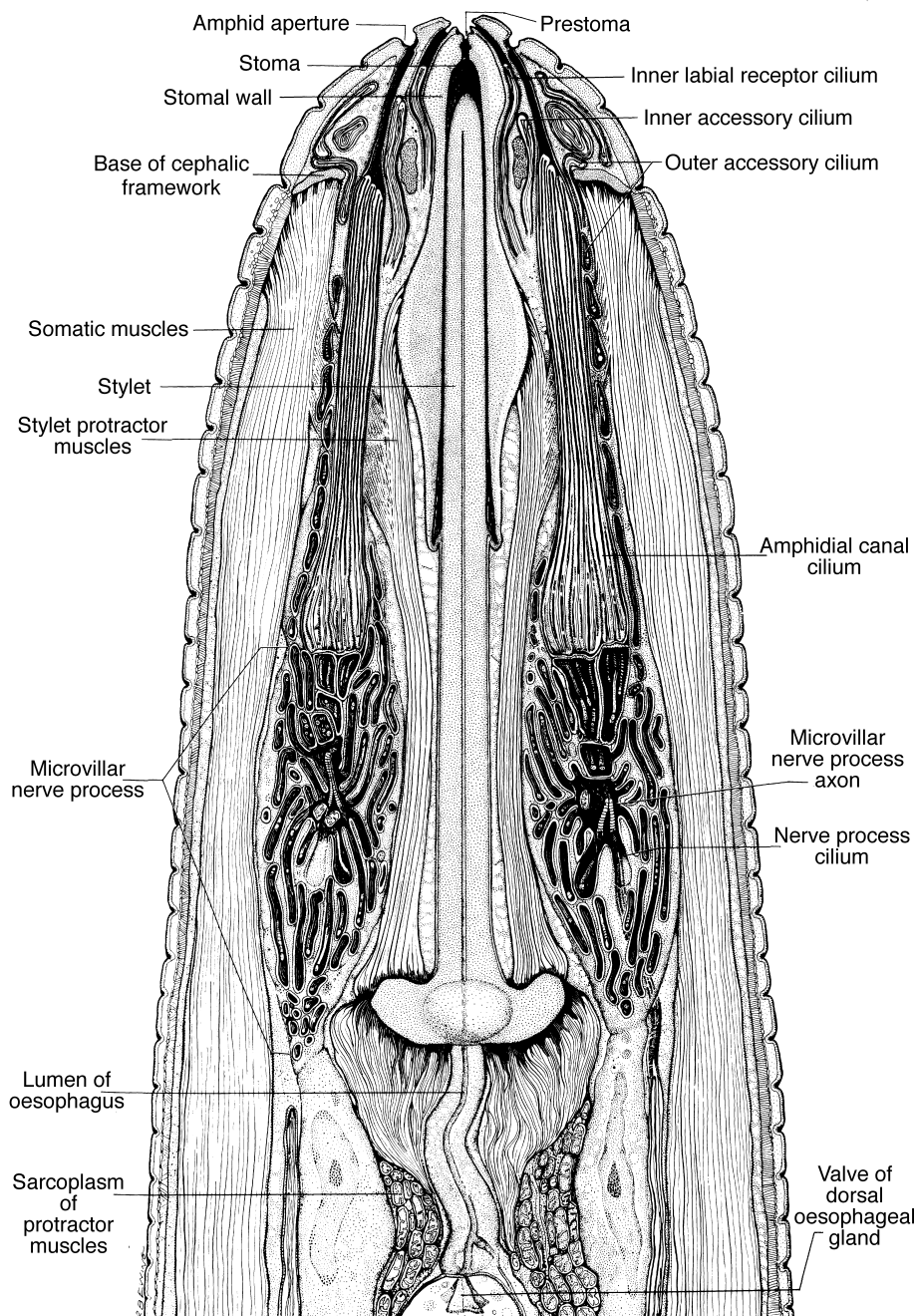
The oral or stomatal opening is minutely rounded (Tylenchidae, *Meloidogyne* females, etc.) or dorso-ventrally oval or slit-like (most Hoplolaimidae, Meloidogynidae and Heteroderidae males, etc.). In Criconematina, the two lateral oral liplet-like structures make the oral opening look I-shaped.

### Pseudolips or lip areas

There are no lips in Tylenchida except for the two lateral liplet-like structures at the oral opening in Criconematina. The areas surrounding the oral opening and bearing labial sensilla are the true 'lips', generally modified to form an oral or labial disc (Fig. 8(d)). Loof & De Grisse (1974) introduced the term **pseudolips** for six lip areas around the oral opening of some Criconematidae.

In *Pratylenchus* spp., the submedian lip areas (since the two subdorsals and two subventrals cannot easily be differentiated in a face view, they are referred to as submedians or medials) and lateral lip areas are fused to the oral disc and the whole represents a **cephalic plate** (Corbett & Clark, 1983).

Stone (1975) illustrated and described six lip patterns of Heteroderidae. The basic pattern is typically hoplolaimoid and bilaterally symmetrical, with an oval labial disc bearing an oval oral aperture, and is surrounded by six pseudolips. The amphid apertures are pore-like on lateral pseudolips at the base of the labial disc. Eisenback & Hirschmann (1979) pointed out that the other patterns result from the various degrees of fusion of the submedial (= submedian) pseudolips with the labial



**Fig. 9.** Structure of the feeding apparatus and cephalic sensory organs of a juvenile of soybean cyst nematode, *Heterodera glycines*. Three of seven amphidial cilia are shown. (After B.Y. Endo (1980): *Journal of Ultrastructure Research*, courtesy Academic Press.)

disc and not by the elongation of the labial disc and subsequent loss of the submedian pseudolips, as suggested by Stone (1975).

In the second-stage juveniles of *Meloidogyne* spp. the labial disc and the submedian lips appear dumb-bell- or bow-tie-shaped, bearing the oval aperture of the prestoma which leads to the slit-like stomatal opening medially below it (Eisenback & Hirschmann, 1979). Six labial papillae or pits are located on the labial disc around the oral aperture and each submedian pseudolip bears an indication of submedian cephalic sensilla. The amphid apertures are transversely elongated, slit-like, at the base of the labial disc. In Pratylenchidae and Hoplolaimidae the four cephalic sensilla also do not show on the surface. The submedian cephalic lobes of Criconematidae are important diagnostic characters, and have originated differently in different groups. The lobes may originate as outgrowths of the submedian pseudolips (*Lobocriconema*), as enlargements of the submedian pseudolips (*Criconemoides*) or as enlargements of the labial disc (*Discocriconemella*).

Sher & Bell (1975) provided SEM *en face* views of several Tylenchina and discussed the taxonomic importance of cephalic structures. Figure 104(b) illustrates how the *en face* view helps in the differentiation of dolichodorid genera. *Neodolichorhynchus* (N.) *microphasms* has broken annules behind amphidial apertures, which is not the condition with *Neodolichorhynchus* (*Mulkorhynchus*) *phaseoli* (cf. Fig. 104(b)A vs. B). Similarly the head has broken annules behind the amphidial apertures in *Telotylenchus ventralis* but not in *Bitylenchus brevilineatus*, *Meiodorus festonatus* and *Trichotylenchus falciformis*. In the same way the shape and position of the labial disc and amphidial apertures in *Trichotylenchus* clearly differentiate it from *Tylenchorhynchus*.

Merliniinae is another group in which genera can easily be differentiated on *en face* characters. Figure 8(f) shows *en face* views of *Nagelus* and *Amplimerlinius* which lack a labial disc and six longitudinal indentations on cephalic annules (Fig. 8(f)B & D) as compared to *Geocenamus* and *Scutylenchus* which have them (Fig. 8(f)A & C). The labial disc of *Geocenamus* is rounded and offset as compared to *Scutylenchus* (and *Merlinius*).

## (ix) Stylet

The stylet or spear of Tylenchida is a **stomatostylet** (= stomatostyle) whereas that of the Dorylaimida is an **odontostylet** (= odontostyle). The stylet is composed of two parts: the anterior **conus** and the posterior **shaft**. The latter bears three (one dorsal, two subventral) **basal knobs**; rarely the knobs may be absent. The tylenchid stylet varies in length from 5  $\mu\text{m}$  to 180  $\mu\text{m}$ . When in the normal position, the stylet tip lies inside the stoma 1–3  $\mu\text{m}$  from the oral opening. The size and shape of the stylet are important diagnostically. The total length of the stylet and the length of its conus and the size and shape of the basal knobs are used in the differentiation of species, as well as to separate genera and higher categories (e.g. stylet knob shape in Criconematoidea vs. Hemicyclophoroidea). Stylet shape in female *Meloidogyne* can be used to differentiate species (Eisenback *et al.*, 1980).

Thorne (1961, p. 75) compared the homologies of the various stoma parts in *Rotylenchus* (Tylenchida) with those in *Rhabditis* (Rhabditida) and *Eucephalobus* (Cephalobida) as originally conceived by Chitwood & Wehr (1934) and Chitwood & Chitwood (1937) and postulated that the prorhabdions formed the conus, the meso- and metarhabdions formed the shaft and the telorhabdions formed the basal

knobs. Andr ssy (1962) suggested that the conus was derived from the metarhabdions and the shaft and the basal knobs from the telorhabdions, calling the two parts of the stylet the **metenchium** and **telenchium** (Fig. 7). Goodey (1964) drew a correlation between the Aphelenchida stylet and the rhabditoid stoma parts, suggesting that the conus represented the fused metarhabdial teeth and that the shaft and the basal knobs were formed by the metarhabdions and telorhabdions, respectively. De Grisse (1972b) supported Goodey's interpretation of the homology between the conus and the metarhabdial teeth, and showed that in tylenchid and criconematid genera pro- and mesorhabdions form a **stylet sheath** which is attached to the base of the conus. De Grisse & Lagasse (1969) found the oesophageal lining penetrating the stylet knobs and forming six longitudinal chords. These chords appear to have been derived from the six cells forming the precorpus.

The conus is more electron-dense than the shaft. It is not a solid cone with a lumen through its long axis, but is double-walled behind the tip, with the main body filled with the shaft material making an interlocking device (Fig. 10C). The shaft and basal knobs consist of a homogeneous material and are part of the living tissue of the oesophagus (Chen & Wen, 1972). The lumen lining of the shaft and knobs is continuous with that of the oesophagus.

### Stylet muscles

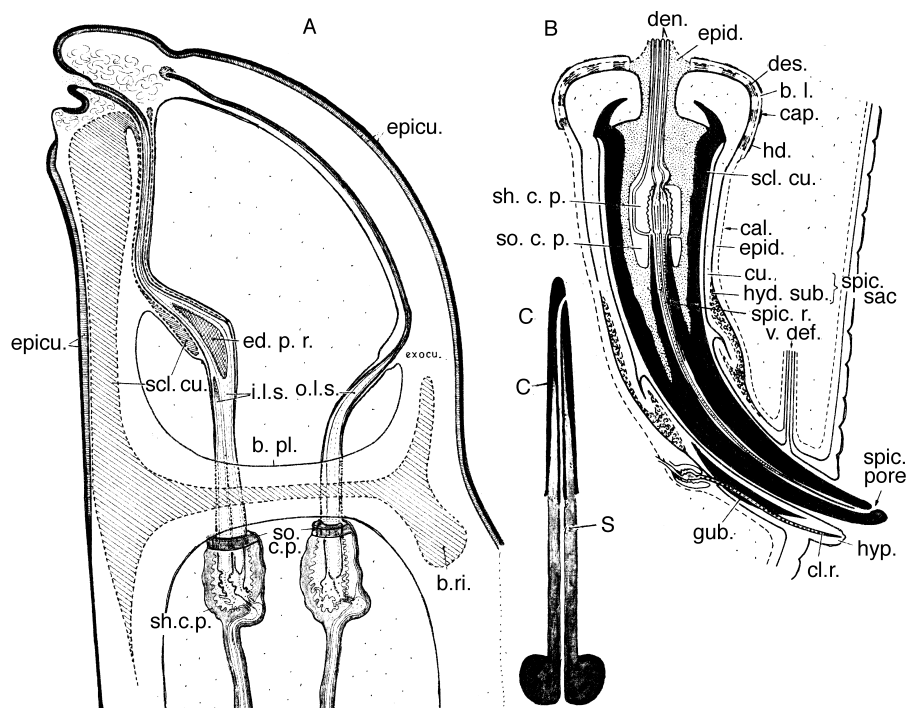
The protractor muscles of the stylet arise from non-contractile oesophageal tissue and are lined by the same basal lamina that covers the oesophagus. In fact, the cell bodies of these muscles lie deep inside the precorpus behind the stylet knobs (Fig. 9). Tylenchida lack retractor muscles for the stylet which is withdrawn after protrusion by the body pressure and the elasticity of the oesophagus.

In *Meloidogyne* and *Heterodera* males there are three protractor muscles which branch anteriorly into ten elements; the nuclei of the three muscles lie in the oesophageal tissue behind the stylet knobs. The contractile portion of each muscle is attached to a stylet knob posteriorly, and anteriorly to the basal lamina surrounding the vestibule extension and body-wall near the basal ring of the cephalic framework. Beside the ten major muscle elements, there are four secondary units, two subdorsals and two subventrals, which appear to be attached posteriorly to the lumen wall of the oesophagus and anteriorly to terminate near the base of the vestibule extension (Baldwin & Hirschmann, 1976).

Protractor muscles of *Ditylenchus dipsaci* (Anguinata) are attached to the cephalic framework and not to the vestibule extension (Yuen, 1967). In *Hexatylus viviparus* they pass through the cephalic framework and are attached to the outer cephalic cuticle. The stylet of this species has the orifice placed about 1  $\mu\text{m}$  from the tip on the ventral side. The three basal knobs bifurcate, producing six flanges, to which three protractor muscles are attached; the cell bodies of the muscles are embedded in the oesophageal tissues just behind the stylet base (Shepherd & Clark, 1976).

### (x) Oesophagus (Pharynx)

The simplest oesophagus is found in Hexatylinea. *Hexatylus viviparus*, a fungus feeder, has a straight tubular oesophagus lacking musculature and having a circular (not tri-radiate) lumen throughout its length. The lumen, lined by the cuticle, is of the same



**Fig. 10.** A. Longitudinal section through a head sector of a hoplolaimoid nematode (diagrammatic) showing inner and outer labial sensilla. B. Lateral view (diagrammatic) of tylenchid spiculum and gubernaculum showing spicular and cloacal sensilla. (A, B. After Coomans & De Grisse (1981), courtesy Academic Press.) C. Schematic drawing of *Pratylenchus* stylet showing interlocking conus (= tooth) and shaft. (After Chen & Wen, 1972.) (b.l., basal lamina; b.pl., basal plate; b.ri., basal ring of cephalic frame work; C, conus (tooth); cal., calomus; cap., capitulum; cl.r., cloacal receptor; cu., cuticle; den., dendrite; des., desmosomoid; ed.p.r., electron-dense part of receptor; epicu., epicuticula; epid., epidermis; exocu., exocuticula; gub., gubernaculum; hd., hemidesmosome; hyd.sub., hydrostatic substance; hyp., hypostygmia; i.l.s., inner labial sensillum; o.l.s., outer labial sensillum; S, shaft; scl.cu., sclerotized cuticle; sh.c.p., sheath cell process; so.c.p., socket cell process; spic.pore, spicule pore; spic.r., spicule receptor; spic.sac., spicular sac; v.def., vas deferens.)

cross-sectional area as the stylet lumen (c.  $0.02\text{--}0.03\ \mu\text{m}$ ). The oesophago-intestinal valve is located anterior to the nerve ring. The oesophagus in this nematode is not syncytial, as in many animal-parasitic nematodes, and the oesophageal glands form a diverticulum overlapping the anterior intestine. The subventral and dorsal oesophageal glands open into the oesophageal lumen anterior to the oesophago-intestinal junction and at the base of the stylet, respectively (Shepherd & Clark, 1976). Throughout the Tylenchida, the dorsal gland orifice is located in the precorpus, often close ( $1\text{--}3\ \mu\text{m}$ ) to the stylet base.

In several Hexatyline, and in all Tylenchina, Hoplolaimina and Criconematina, the oesophagus has a distinct corpus, isthmus, and a basal bulb or gland lobes. In

most Tylenchida, the corpus is divided into **precarpus** and **postcarpus** (the equivalent terms **procarpus** and **metacarpus** are hybrids between Greek and Latin words and are not used here; the term postcarpus has been incorrectly used for the basal region of the oesophagus lying posterior to the corpus and isthmus and this practice should be discouraged). The precarpus has six cells, enclosed by a basement membrane, running longitudinally from the median bulb to the base of the stylet. The lumen of the precarpus is circular.

The postcarpus or median oesophageal bulb is muscular in most *Hoplolaimina* and all the *Criconeematina* (except males and some juveniles). In *Pratylenchus penetrans*, at the position of the valvular apparatus of the median bulb, the lumen is distinctly triradiate, but anterior to it the lumen is circular. The median bulb has six muscle cells attached to the dorsal and lateral sides of the lumen wall; their myofibrils fan out to the periphery attaching to the basement membrane that forms the outer covering of the median bulb. In addition, there are six other cells, interspersed with the six muscle cells. Two subventral gland ampullae open just behind the valvular apparatus into the lumen of the bulb. The lumen of the isthmus is triradiate (Chen & Wen, 1972).

The median bulb of *Hoplolaimus* consists of 15 cells – six muscle, three marginal and six nerve cells. The isthmus is composed of nine cells whose cell bodies lie near the oesophago-intestinal junction (Grootaert *et al.*, 1976).

### Oesophageal glands

The Tylenchida have three uninucleate oesophageal glands (salivary glands), one dorsal and two subventral. The dorsal gland of *Basirolaimus* spp. has four nuclei, and each of the subventral glands of females of some *Meloidogyne* spp. (e.g. *M. cruciana*) has two nuclei. The glands may either be enclosed in a basal (terminal) bulb, or lie free in the body cavity extending over the intestine.

The oesophageal glands remain separate or may fuse into a syncytium (e.g. *Heterodera* and some *Pratylenchus* spp.). They are narrow in *Atalodera* and *Thecavermiculatus* as compared to cyst-forming Heteroderinae, in which they are usually broad, filling the body cavity. The gland lobe of *Hoplolaimus* consists of cell bodies of the glandular cells, nerves and cells of uncertain nature, perhaps epidermal in origin. The glands are under neuro-sensory control, with active synthesis of secretory products occurring in the posterior region, with anterior parts serving as storage (Grootaert *et al.*, 1976). The oesophagus of *Heterodera glycines* and *Meloidogyne incognita* is supplied with nerve processes originating from the ganglia associated with the nerve ring, as well as from perikaryons within the median bulb (Baldwin & Hirschmann, 1975).

From the dorsal and subventral glands arise separate ducts which extend forward and form an ampulla before opening into the lumen of the oesophagus through cuticularized branched tubules. There is a complex end-apparatus (collecting and releasing mechanism) at the dorsal gland outlet forming a one-way valve which is probably controlled by the nerve that abuts the dorsal surface of the ampulla (Anderson & Byers, 1975).

The subventral glands are probably concerned with the penetration of the host tissue since they are enormously developed in pre-parasitic females of Hexatylinina that invade insects, and second-stage juveniles of Heteroderidae and Meloidogynidae

that invade roots. In the latter, when a feeding site is established, the subventral glands secondarily become atrophied and the dorsal gland enlarges as feeding commences. The granules in the subventral gland ampullae are different in structure from those in the dorsal gland ampulla (Bird, 1968). During feeding of *Bitylenchus dubius*, a salivation phase, involving flow of dorsal gland secretion into the food cell, is followed by an ingestion phase, when the postcorporate pump acts rhythmically for up to 12 min (Wyss, 1973).

Siddiqi (1971) and Seinhorst (1971) discussed the importance of the arrangement of the oesophageal glands in the systematics of Tylenchida. According to Siddiqi (1971), the subfamily Hoplolaiminae contains forms which have oesophageal glands extending over the intestine dorsally and dorso-laterally whereas in Rotylenchoidinae and Rotylenchulinae the glands extend over the intestine ventrally or ventro-laterally. In Tylenchina, a basal bulb enclosing the glands is found in the families Tylenchidae, Psilenchidae and Dolichodoroidae, and in these groups, if the glands extend over the intestine, it is the dorsal gland that becomes enlarged and lobe-like. In the families Hoplolaimidae, Heteroderidae and Meloidogynidae, the glands extend over the intestine, with the subventral glands primarily enlarged and extending past the dorsal gland.

Anderson in Geraert (1976) is said to have indicated that, in *Helicotylenchus*, the oesophageal glands tend to be separate and the oesophago-intestinal valve is less developed than in other hoplolaimids, giving greater plasticity and consequently variability in position with respect to the intestine. Geraert (1976) transferred *Rotylenchus orientalis* Siddiqi to *Helicotylenchus* on the basis that the structure and overlap of the oesophageal glands correspond more to those described in *Helicotylenchus* than in *Rotylenchus*. However, Sher in Geraert (1976) believed that this species represented a new genus for which the name *Orientylus* was proposed by Jairajpuri & Siddiqi (1977). The arrangement of the oesophageal glands was the basis on which Sher (1973) discussed the phylogenetic relationship of the monodelphic *Apratylenchoides* with the didelphic *Pratylenchoides* and de Guiran & Siddiqi (1967) differentiated *Zygotylenchus* from *Pratylenchoides*.

### Oesophago-intestinal valve

The oesophago-intestinal valve or **cardia** is also lined internally with cuticle. *Hexatylys viviparus* has a valve consisting of small extensions from **two cells of the oesophagus**, at the oesophago-intestinal junction. Some microtubular elements are present in the valve cells (Shepherd & Clark, 1976). In Tylenchoidea, the valve is prominent and three-celled in forms having a basal oesophageal bulb. In Pratylenchidae, Heteroderidae and Meloidogynidae, the valve may be extremely reduced, although its tricellular nature may be detectable in TEM sections.

*Hexatylys viviparus* has no specialized oesophago-intestinal valve cells. Geraert (1992) following Shepherd & Clark (1976) stated that the valve consisted of extensions of two oesophageal cells; a pair of uninucleate anterior intestinal cells quite different from the mid-intestinal cells. The valve in *Ditylenchus dipsaci* is indistinct, being enveloped by the basal oesophageal bulb. There are two extremely small cells in this valve as revealed by TEM (Shepherd & Clark, 1983).

## (xi) Intestine

The intestine may be cellular or syncytial and oligocytous (when only few (two to five) cells are present in a circumference) or polycytous. Its inner walls may be lined with a bacillary layer of microvilli. The intestine in Criconematina and most adult Hoplolaimina is syncytial and the intestinal lumen is not detectable. The **anterior intestine** (ventricular region) is the anteriormost region of the intestine, which in *Hexatylus viviparus* is about 80  $\mu\text{m}$  long, very narrow with a lumen of only 1  $\mu\text{m}$  in diameter, and is lined with short, stubby microvilli. The anterior intestine is constructed of two cells, one dorsal, the other ventral, each semi-circular in cross-section. The **mid-intestine** is the largest part and extends from the anterior intestine to the rectum. In *H. viviparus* it has a wider lumen lined with longer microvilli than those in the anterior intestine. The cells of the mid-intestine overlap and encase the anterior intestine for about 20  $\mu\text{m}$  (Shepherd & Clark, 1976). Unlike root-feeding species of Tylenchina, *H. viviparus* lacks a **prerectal valve** and hence a closable **rectum**. It has a well-defined rectal cuticular lining and associated muscles which make the rectum a pumping organ. The rectal pumping action makes about ten defecation cycles every 15 to 20 min and keeps the body pressure low during feeding on fungal hyphae. The nematode lacks an oesophageal feeding pump and is passively fed, partly by the turgor pressure within the food cell (fungal hypha) and partly by the pumping action of the rectum (Doncaster & Seymour, 1975; Seymour, 1975). Passive feeding and rectal pumping action may occur in other Hexatylinea.

In *Ditylenchus dipsaci* there are 20–30 intestinal cells with microvilli which lie in pairs, forming dorsal and ventral rows. The cells generally alternate and hence the intestinal lumen is sinuous. In *Triversus* (= *Tylenchorhynchus*), the intestinal cells lie in pairs (probably 12–15), forming dorsal and ventral rows. Fasciculi found in several dolichodorids are fibrillar bundles having thin filaments and thick rod-like elements (Geraert, 1992). In advanced root parasites, such as *Heterodera* and *Meloidogyne*, the intestine becomes a storage organ. It lacks microvilli and hence probably there is no release of enzymes and digestion is entirely extracorporeal. The lumen wall without microvilli is too thin and hence the intestinal lumen in these genera has often been reported as absent.

*Meloidogyne* spp. have six large **rectal glands** which produce a gelatinous matrix in which eggs are deposited. The **anus** in Tylenchida is a minute pore facing outward. In other orders of Secernentea including Aphelenchida, Rhabditida, Diplogasterida and Cephalobida, the anus is a large, crescentic slit-like aperture directed posteriorly.

## (xii) Tail

Nematodes differ from other metazoa, except lower chordates, in having a true tail, i.e. postanal elongation of the body. The tail is elongate-filiform in Tylenchidae, prehensile in Halenchidae and variously modified in other groups. Its shape may differ between juveniles and adults or between the two sexes. The primary function of the tail is to assist in locomotion, but it may also aid in anchorage (e.g. prehensile tail of *Halenchus* and during copulation) and in the exit of the juvenile from the egg-shell.

In a large number of genera in which the tail is short (Hoplolaimidae) or absent (Heteroderidae, Meloidogynidae) in adults, the tail is generally well developed in



juveniles. The male tail in several genera is enveloped by a bursa and is conical, being different in shape from that of the female. The male tails of Dolichodorinae and Meiodorinae have a large trilobed bursa and the female tails are elongate, fili-form, spicate, mammillate or hemispherical. The males of most Tylenchuloidea lack a bursa and have a tail similar in shape and size to that of the second-stage juveniles. The migratory preadult females of *Rotylenchulus* have a differently shaped and longer tail from that of their juveniles. In *Tylenchulus* and *Rotylenchulus*, in which the female is swollen, the tail shortens during the development but later elongates in the preadults. The mean tail length increases with body length during post-embryonic growth in several genera (Geraert, 1979). The male tail of *Tylenchulus semipenetrans* has two almost terminal setae (Coomans & De Grisse, 1981).

### (xiii) Female Reproductive System

The female in the suborder Hoplolaimina is didelphic (Greek *di* = double, *delphys* = uterus, womb). Occasionally the posterior branch is reduced in size or represented by a postvulval uterine sac (Pratylenchidae, *Rotylenchoides*, *Trophurus*). The female in the suborders Tylenchina, Hexatyline and Criconematina is monodelphic (Greek *mono* = single, *delphys* = uterus). In the didelphic female, the two branches of the reproductive system are outstretched in opposite directions from the vulva, being amphidelphic or, as in Heteroderidae, prodelphic; in monodelphic forms, the gonoduct is always prodelphic.

### Vulva

The female gonopore or vulva is a transverse slit-like aperture which may be transversely oval but rarely round, located on the ventral side of the body (slightly shifted from the midventral line in *Cephalenchus*). It is usually a large slit but can be small in some genera (*Gymnotylenchus*). In didelphic forms it is generally median or submedian but in obese females may become terminal or subterminal. In monodelphic forms it often lies near the anus (Hexatyline and Criconematina). Bivulvarity is a rare phenomenon and an abnormality but it has been seen in *Scutellonema bradys*, *Meloidogyne javanica* and *Hoplolaimus indicus* (see Varma *et al.*, 1977).

Lateral vulval membranes were used to diagnose the genus *Pterotylenchus* (see Fig. 8(a)C). They are also useful in recognition of *Cephalenchus* and Tylenchidae, but they may or may not be present in the genera *Coslenchus*, *Helicotylenchus* and *Neodolichorhynchus*. The anterior lip of the vulva may extend over the vulva, as in *Criconema*, or may form a longitudinal flap over it, as in *Atylenchus*. The **epiptygma** (pl. epiptygmata) is a cuticular, membranous structure and is located on the vagina or on the vulval lip. Epiptygmata are commonly found in Hoplolaimoidea. In *Peltamigratus* and *Scutellonema* spp. epiptygmata may project and become conspicuous. In *Helicotylenchus* they lie inwardly folded deep in the vagina, but in *Rotylenchus* they are placed near the vulva. In *Ditylenchus dipsaci* there are two epiptygmata directed dorsally at the distal wall of the vagina. The position of the vulva on the body, the presence/absence of lateral vulval membranes and epiptygma are important diagnostic characters.

## Vagina

The vagina (a passage leading from the vulva to the uterus) is thin- or thick-walled, usually leading inwards at right angles to the body axis, but may be directed forward, especially in monodelphic forms. The vagina of *Ditylenchus dipsaci* is a flattened tube provided with eight **dilatores vaginae** and two **constrictores vaginae** muscles. The vagina of *Amplimerlinius icarus* has two anterior and two posterior inner dilatores vaginae and **directores vaginae** (De Grisse & Roman, 1974). The eight dilatores vaginae of *Tylenchulus semipenetrans* are comparable with those of other criconematids (Natasasmita & De Grisse, 1976).

The female reproductive branch (= gonoduct, genital tract) comprises uterus, uterine crustaformeria (= shell gland, columella, pre-uterine gland), spermatheca, oviduct and ovary. The cells of the genital duct adhere to each other by means of an interlocking device, the 'zipper'-fasciae adhesion system (De Grisse & Roman, 1974).

## Uterus and crustaformeria

In *Pratylenchus* spp. the uterus is in the form of a tube lined with flat cells and is muscular and extensile. Posterior to the vulva it extends into a sac which may carry a tricolomellate **crustaformeria** and a vestigial ovary (*P. coffeae*, *P. zeae*) (Roman & Hirschmann, 1969). At the distal end is a **tricolomella** of 12 cells in three rows of four cells each. A tricolomella is also present in *Amplimerlinius icarus* and *Tylenchorhynchus* spp. The crustaformeria of *Ditylenchus* has four rows of four cells each, hence it is called **quadricolomella**. De Grisse & Roman (1974) and Geraert (1983) found two cells of unknown function between the uterus and spermatheca in *Amplimerlinius icarus* and *Tylenchorhynchus* spp. Chizhov (1981) found the pre-uterine gland of Heteroderidae variable, the more specialized forms having the greater number of rows and cells, i.e. 30 to 35 cells in three rows in *Heterodera avenae*, 120 to 220 cells in four rows in *H. glycines* and 180 to 360 in up to eight rows in *Globodera rostochiensis*.

## Spermatheca

In bisexual species of Hoplolaimina the **spermatheca** (= spermatheca) (plural: spermathecae) is usually round and axial; the eggs do not mature if no sperm are present in the spermatheca to fertilize them. In parthenogenetic species it is small and empty (wrongly referred to as a spermatogonium by some workers), but in bisexual impregnated females it contains elongated sperm, each consisting of a granulated nucleus and a hyaline 'tail' portion (Roman & Hirschmann, 1969). The spermatheca of *Pratylenchus* spp. is composed of about ten epithelial cells. In *Tylenchorhynchus* sp. the spermatheca is made up of 12 cells, more or less in four rows (Geraert, 1983). Criconematina have a ventrally placed spermatheca which is a thin-walled sac in the anterior end of the crustaformeria. Hexatyline and Anguinoidea have an axial spermatheca, often well elongated in free-living forms. In entomoparasitic partially free-living preadult females the sperm may be dispersed throughout the length of the exceedingly long uterus, but in the adult parasitic female, the sperm are localized and appear to be lodged in thin-walled uterine cells (e.g. *Contortylenchus* spp.).

### Oviduct and ovary

In Tylenchida there are two rows of three or four flattened cells, tightly packed to act as a valve between the spermatheca and the oviduct. The oviduct of Dolichodoridae and Hoplolaimoidea is formed from two rows of four cells. The oviduct of *Hexatylys viviparus* consists of two consecutive rings of four cells each (Geraert, 1976a). The ovary has a germinative or multiplication zone, a growth zone and a ripening zone (the empty region which becomes filled with ripening eggs). The germ cells are proliferated only at the tip of the ovary, hence the latter is called **telogonic** (cf. **hologonic** when the germ cells are proliferated over the entire length of the ovary).

Egg-shell formation was studied by McClure & Bird (1976) in *Meloidogyne javanica*. Oogonia are radially arranged around a central rachis, to which they are attached by cytoplasmic bridges. The oocytes pass in tandem through the oviduct of two rows of four closely packed cells and into the spermatheca where egg-shell formation begins with the modification of the oolemma to form the vitelline layer. The chitinous layer begins to form in the distal portion of the uterus and probably originates from the egg. Proline-containing protein is deposited in the chitinous and lipid layers as the egg passes through the mid-region of the uterus and formation of the lipid layer in this region completes egg development.

### (xiv) Male Reproductive System

Members of the Tylenchida are monorchic, i.e. have only one testis, except some *Meloidogyne* spp. which occasionally have two testes due to sex reversal. The testis is outstretched, or reflexed at the tip due to growth in length greater than the space available to contain it. Spermatocytes are arranged in one, two or multiple rows, rarely about a rachis as in *Anguina*. The sperm are continuously produced by adult male Tylenchina, but in all the genera of Criconematina and of some Hexatylyna they are produced at one stage of development, possibly just before the final moult; in adults of such forms, the testis appears degenerate but well-formed sperm pack the gonoduct. The male gonoduct joins the rectum and opens through a common pore called the **cloacal aperture**.

### Male accessory genital structures

The **bursa** (bursa copulatrix, caudal alae) is usually present in Tylenchida and differs from that of other orders in lacking papillary ribs formed by the extension of the caudal papillae. However, in Tylenchina, phasmids may extend into the bursa flaps and form **pseudoribs**. It may be adanal (just around the anal region), subterminal (= leptoderan) or terminal, enveloping the entire tail and not just confined to the terminal portion of the tail (= peloderan). The bursa flaps may be simple, convex, or modified to become lobed, pointed or rectangular. The bursa margins may be smooth or crenate.

### Spicules

Spicules are cuticular structures similar to the stylet conus in electron density and develop by a gradual thickening and invagination of the posterior walls of the spicular pouches which originate from the primordium of the rectal epithelium. They are sensory structures which also serve as an aid in the transfer of sperm to the female

genital tract. They are paired, ventrally arcuate or curved, generally similar, cephalated and independently retractable, except for Iotonchiinae. The spicule is a simple structure, being tubular with nerves passing through its lumen and ending in a sense organ open at the tip, generally ventral, but also terminal or dorsal (Fig. 10B). In several genera the spicules have ventral or subventral **flanges** or **vela** (singular velum) and together, when protruded, form a tubular passage for the sperm (Fig. 108(b)E). On this basis, the spicules in the subfamilies Telotylenchinae and Merliniinae are quite different from each other (cf. Fig. 108(b)E & F).

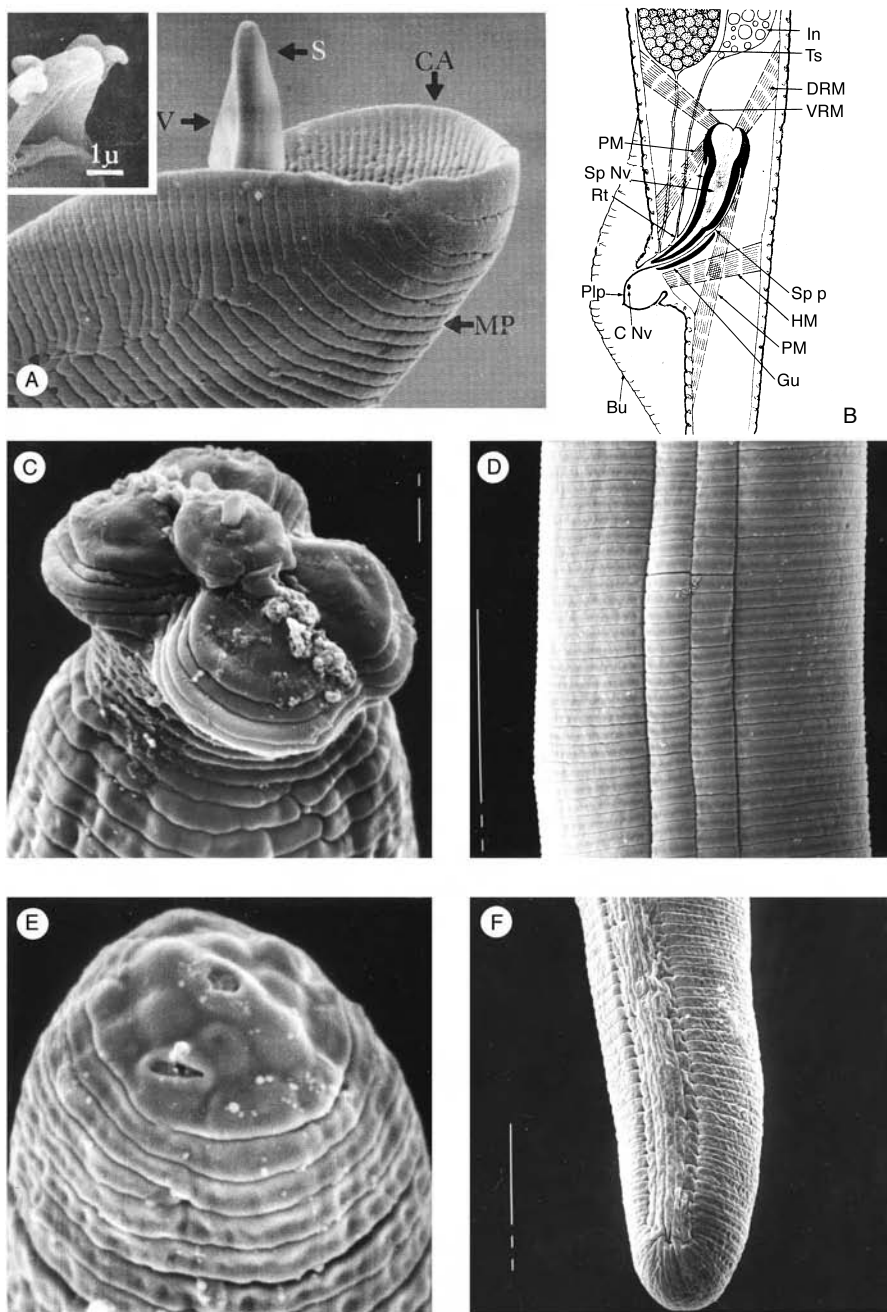
In *Hoplolaimus galeatus* the spicules are dimorphic; only one spicule, the outer one, has a velum which completely surrounds the inner spicule; the tip is narrow and has a terminal pore (see Fig. 11A) (Högger & Bird, 1974).

The spicules of *Pratylenchus penetrans* are also dimorphic, the outer being slightly larger than the inner spicule. The spicular core is filled with nerve tissue and the tip has two pores, each pore with one dendritic element (see Fig. 11B) (Wen & Chen, 1976). The number and location of the terminal pore(s) of spicules also have taxonomic significance and require further study. For example, *Heterodera* spp. have two terminal pores and *Globodera* spp. have one. The shape of the spicule and its tip is one of the differentiating characters between Merliniinae and Tylenechorhynchinae (see also Coomans & De Grisse, 1981).

Electron micrographs of serial sections show that *Scutellonema brachyurus* has two morphologically identical spicules. Each is composed of a swollen tubular head, crescentic shaft, and leaf-like blade with membranous velum expanded from the central trunk. The spicules are concave and grooved on the ventral side and convex on the dorsal side near the trunk. Nerve tissue in the core of the spicule has a dendritic process which gains access to the exterior via a small pore on the lateral side of the spicule tip. Three protractor and two retractor muscles are associated with each spicule. A sensory accessory piece connects with the tip of the gubernaculum and protrudes from the lower side of the opening of the spicular pouch; it protracts and retracts with the muscularized gubernaculum. The gubernaculum, in this species, varies from bow-shaped in the distal part to boat-shaped in the mid-region. It is mobile by muscles of the protractor gubernaculi, retractor gubernaculi and seductor gubernaculi (Wang & Chen, 1985).

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**Fig. 11. opposite** A. Scanning electron micrograph showing lateral view of male caudal region of *Hoplolaimus galeatus*. Inset: protruded gubernaculum tip with titillae. (CA, caudal alae; S, spicule; MP, microprojections (longitudinal row of dots); V, velum. Note terminal indentation or pore of spicule. (After Högger & Bird (1974), courtesy *Journal of Nematology*.) B. Schematic drawing of spicule region of *Pratylenchus penetrans* male. Bu, bursa; C Nv, cloacal nerve; DRM, dorsal rectal muscle; Gu, gubernaculum; HM, H-shaped muscle; In, intestine; Plp, posterior lip of cloaca; PM, protractor muscle; Rt, rectal terminus; Sp Nv, spicular nerve; Sp p, spicular pouch; Ts, testis; VRM, ventral retractor muscle. (After Wen & Chen, 1976.) C and D. Scanning electron micrographs of *Dolichodorus minor* Loof & Sharma, female from Costa Rica. C. Head end. D. Lateral field. E and F. Scanning electron micrographs of *Amplimerlinius macrurus* (Goodey), female from England. E. Head end. F. Tail end. (Long line in C = 1  $\mu\text{m}$ , in D and F = 10  $\mu\text{m}$ .)



## Gubernaculum

The thickening and sclerotization in the dorsal wall of the spicular pouch forms the gubernaculum while the **telamon** (= **capitulum**) as a part of the gubernaculum develops in conjunction with the ventral wall of the cloaca (Baylis & Daubney, 1926). The gubernaculum is generally plate-like and may have two grooves in which the spicules glide during copulation. Between these grooves may be formed a median piece called the **cuneus**, joined to two lateral pieces called **crura**. In *Pratylenchus penetrans* the gubernaculum is similar to the spicules in electron density and does not communicate with the spicular pouch but lies embedded and fixed in its cuticular wall. It is immovable and not supplied with muscles. There is no telamon in this species (Wen & Chen, 1976). The gubernaculum of *Hoplolaimus galeatus* is protrusible and has two lateral bilobed **titillae** at the distal end. When the spicules are completely retracted, the gubernaculum tip and titillae remain visible (Högger & Bird, 1974). In *Rotylenchus* there are sensory receptors that end in the titillae (Coomans & De Grisse, 1981).

## Spicular and gubernacular muscles

Coomans (1962) described spicular and gubernacular muscles of *Rotylenchus goodeyi*. There are two protractors and two retractors for each spicule. External protractor muscles extend from the external side of the spicule head to the latero-ventral side of the body-wall. The internal protractor muscle extends from the internal side of the spicule head to the telamon; its identity as a separate muscle is doubtful. Latero-dorsal and latero-ventral retractor muscles extend from the head of the spicule to the body-walls, respectively between the latero-dorsal and latero-ventral somatic muscle field and the lateral chords.

The **protractor gubernaculi** extends from the proximal part of the gubernaculum to the subventral body-wall and the **retractor gubernaculi**, a large subdivided muscle, extends from the distal part of the gubernaculum to the lateral body-wall. The **seductor gubernaculi** is another muscle that extends from the proximal end of the gubernaculum to the latero-dorsal or latero-ventral body-wall. The shape and size of the spicule and gubernaculum, the presence of a telamon and titillae and the protrusibility of the gubernaculum are used in the identification and classification of the Tylenchida.

## Cloacal lips and genital papillae

The cloacal lips are generally rounded, but may be raised, pointed or drawn out into a **penial tube** (**tubus**) (e.g. *Hemicycliophora*, *Aulosphora*). The genital papillae (one to four) are grouped around the cloacal aperture; they may be absent. There are no male caudal papillae in Tylenchida, except for *Fungitonychium*, in which a large stump-like papilla is found on the midventral side of the tail, a little behind the cloacal aperture. The paired genital papillae on the posterior lip of the cloacal aperture of Merliniinae have been named **hypoptygma** (pl. hypoptygmata) by Siddiqi (1970). In members of the superfamilies Criconematoidea and Hemicycliophoroidea there is a single, often setose, papilla on the posterior lip of the cloaca.

## 2. TAXONOMIC METHODS

Taxonomy is a fundamental science which deals with the recognition of taxa, and systematics is a method of classification or pigeon-holing of taxa in a hierarchical system through defining groups and determining their ranking. Because the subject matter covered by both terms overlaps greatly, they usually mean the same thing.

Identification involves naming of taxa, mostly at generic and species levels, using taxonomic characters. In Tylenchida, taxa are recognized and classified mainly on morphological characters. It is only recently that ecological, physiological, biochemical, cytological and embryological characters are beginning to be introduced, but in a very limited manner. The use of DNA and mitochondrial probes, protein characterization by immunoelectrophoresis and monoclonal antibodies in identification of species, subspecies and races/pathotypes is gaining momentum. The behaviour and ecology of Tylenchida have sometimes formed the basis of classification (Jones, 1965; Williams, 1968), and Hooper (1969a) and Mai & Lyon (1975) have used them in differential keys for plant-parasitic groups. Russell (1987) reviews root-observation techniques and describes a simple and high-resolution, *in vitro* root-observation method which helps one to study under high magnification nematode behaviour and host-parasite relationships. Behavioural characters are more prone to convergent and parallel evolution than the morphological ones. Taxa at the species level are based on populations whose morphology and behaviour can be studied, but at higher levels they are subjective, being names of groups formed to fulfil a need.

Luc (1989) stressed the point that easily observable characters used in simple identification keys, such as obesity of sedentary females, number of female genital branches, number of incisures in the lateral field, etc., need to be separated from taxonomic/systematic characters. This is particularly important in the characterization of suprageneric taxa. For example, the grouping of genera with obese bodies in Heteroderoidea by Golden (1971), the use of the presence of one or two female genital branches in the system of classification given by Andr  ssy (1976) and the characterization of Neotylenchoidea Thorne, 1941 by a non-valvular median oesophageal bulb, as done by many workers, had to be rejected. Dichotomous and tabular keys are useful tools in the identification of nematodes and these need updating (which is seldom done) when more taxa are added. Unlike these keys, computer-aided identification keys use several distinguishing characters, are more reliable and can continuously be updated. Diederich *et al.* (2000) give a review of computer-aided tools used in nematode identification and discuss problems associated with computer identification and their possible solutions.

The taxonomy and classification of animals and plants are governed by certain rules of nomenclature. Zoological nomenclature is independent of botanical nomenclature and vice versa. The tenth edition of Linnaeus' *Systema naturae* of 1758 (considered published on 1 January) is the starting point for valid zoological nomenclature and for the consistent application of binominal nomenclature, while Linnaeus' *Species Plantarum* (1753) (starting point date 1 May, 1753 for most plants as per Article 13 of the International Code of Botanical Nomenclature, *vide* Voss *et al.*, 1983) is the beginning of botanical nomenclature. The Linnaean binominal system was consistent, concise and practicable and has been in use ever since. Around that

time, 4400 species of animals were named. The wheat-gall nematode was known to Linnaeus by 1767 (see under 'Historical Review'). Linnaeus believed that there were as many species at the Creation as existed at his time. But in his later years, he tended to believe that species were less rigid and that only broader groups had been originally created, and also that hybridization had, over a period of time, modified the species (Knight, 1981).

In zoology, the naming of the taxa from subspecies to superfamily is governed by the **International Code of Zoological Nomenclature (ICZN)**, which is a collection of rules and recommendations previously adopted by the International Congress of Zoology. The judicial body that looks after the interpretation and implementation of this Code is the International Commission on Zoological Nomenclature which was previously constituted by the International Congress of Zoology. In 1972, the XVII International Congress of Zoology held at Monaco decided to transfer the responsibility for future Codes (and the Commission) from the International Zoological Congresses to the International Union of Biological Sciences (IUBS). The IUBS undertook this responsibility at their XVIII General Assembly held at Ustaoset (Norway) in 1973 under the provisions of Article 76(c). The International Congresses of Zoology still remain the source of authority from which the International Commission on Zoological Nomenclature derives its powers and its constitution (Article 76(a)). The XX General Assembly of the IUBS adopted in 1982 the revised edition III (editions I and II were published in 1961 and 1964, respectively) of the International Code of Zoological Nomenclature which was produced and published in February, 1985 by the International Commission on Zoological Nomenclature under the aegis of the International Trust for Zoological Nomenclature (c/o The Natural History Museum, Cromwell Road, London, SW7 5BD, UK) in association with The Natural History Museum, London. The Code does not cover categories above the superfamily rank, and the infrasubspecies categories (variety, forma, pathotype) are not recognized. It has nothing to do with the ranking of taxa, which is left to the systematists to determine.

The name of the species is binominal, consisting of two words (generic and specific); the subspecies name is trinominal (ICZN Article 5(b)). The name of a subgenus can be cited in parentheses between the generic and specific names but is not counted as a part of either binominal or trinominal names (Article 6(a)). However, such a citation does mean that the subgenus name has been combined with the name of the species or subspecies. Genus- and species-group names should appear in italics or in a type face different from that of the text, the generic name beginning with a capital and the specific name with a lower-case letter. All the names in supra-generic categories are uninominal, i.e. made up of one word, begin with a capital letter, and are not italicized. Species-group and suprageneric names are always written in full.

The taxon *parvus* was proposed by Micoletzky (1922) as a subspecies of *Tylenchus filiformis* Bütschli, 1873. Its systematic position in the animal kingdom is shown in Table 2.



**Table 2.** Systematic position of *Tylenchus filiformis parvus*.

Taxonomic category	Suffix	Name
Kingdom	variable	Animalia
Phylum	-a	Nematoda
Class	-ea	Secernentea
Subclass	-ia	Tylenchia
Order	-ida	Tylenchida
Suborder	-ina	Tylenchina
Superfamily	-oidea	Tylenchoidea
Family	-idae	Tylenchidae
Subfamily	-inae	Tylenchinae
Tribe	-ini	Tylenchini
Genus	variable	<i>Tylenchus</i>
Species	variable*	<i>filiformis</i>
Subspecies	variable*	<i>parvus</i>

\* If a Latin or Latinized adjectival or participial name, it must agree in gender with the generic name (ICZN Article 34(b)).

Systematics, as defined by Matil *et al.* (1987), is 'the study and the description of the diversity of living organisms, the search for nature and causes of their differences and resemblances, the assessment of their relationships and the setting up of a classification reflecting such relationships'.

A classification can be artificial, arbitrary or special if it is produced to fulfil particular needs, such as indexing, cataloguing, information storage and retrieval. Classifications aimed at 'easy' identifications also fall into this category. A natural classification, on the other hand, is based on phylogenetic relationships and tries to show lineages. This type of classification is extremely difficult to achieve since the natural course of organic evolution can only be inferred not determined, but any degree of achievement would be worthwhile. At least we should try to develop a 'close to natural' classification which we hope would be stable and carry most predictive value.

The monothetic concept (vs. polythetic; terms coined by Sneath, 1962; Greek *mono* = one; *poly* = many; *thetos* = arrangement), based on the use of a single character or feature, often produces ambiguities in classification. A polythetic concept involving the use of several characters provides a firmer basis for the classification of taxa. However, the polythetic concept does not necessarily mean that all the characters or features being used are of equal weight. Monothetic sequential keys, with a single differentiating character in each couplet are simple and useful in identification. Polythetic sequential keys, tabular keys and compendia in which several characters are used, on the other hand, are more informative and valuable in differentiation between taxa.

Evaluation and comparison of similarities and relationships of characters and features in different individuals and taxa, characterization of groups and the determination of their ranking in a system of classification involve methodologies which must be based on a sound philosophy. Siddiqi (1989) wrote, 'Any scientific system of classification whether of animals or of inanimate objects must be based on sound philosophy and methodology. Incorrect and improper philosophy and methodology

yield incorrect and misleading results. There is a system of classifying stars on their brightness and surface temperature, although some of the faintest and tiniest stars could actually be the brightest and largest. The correct methodology to classifying them would be to determine their relative distance, mass and spectral type which gives surface temperature. A classification chart called Hertzsprung Russel diagram is made by using this methodology and thus gives a sound classification of stars.'

The philosophy governing the classification of Tylenchida is based on the theory of organic evolution that infers the history and causation of existing phenotypes. The theory is based on circumstantial evidence which, although lacking direct evidence for our senses, provides a federation of supporting facts from geological history, embryology, ecology, ethology, cytogenetics and comparative morphology.

Taxonomy involves characterization, identification and phylogenetic relationships of the taxa. Morpho-anatomical characters as studied by the light microscope, SEM and TEM are used in the identification or determination of taxa of the lower levels, i.e. species, subspecies and physiological races. Anatomical relationships with the host also provide some useful characters, as do physiological, biochemical and cytogenetic characters. Biochemical approaches to taxonomy, mainly using esterase isozymes to separate species, subspecies and races of only specialized plant-parasitic nematodes, such as *Heterodera* and *Meloidogyne*, are a rapid and inexpensive method, in which species banding patterns are obtained using isoelectric focusing and gel electrophoresis, which detect major bands for comparison. Some bands are common to species of a genus, others may be species-specific. Such methods, as well as DNA-based detection and identification techniques, are being developed further and it is hoped that they will not only provide tools for identification of taxa but will help a great deal towards understanding their inter-relatedness and phylogeny.

The determination of the ranking of taxa in a hierarchic system of classification can be broadly categorized into three types: (i) evolutionary systematics; (ii) cladism; and (iii) phenetics. These methodologies are further discussed below, with a hope that Tylenchida systematists will use them when proposing new or amended systems of classification.

Whereas species are based on populations, the genus and higher taxonomic categories are subjective and largely depend on the differentiating characters as perceived by their proposers. Maggenti (1989a) argues that a genus is a phylogenetic unit that differs from similar and related assemblages of species and reflects an ecological unit that is adapted to a particular mode of life, i.e. a valid genus occupies a niche. This strict definition of a genus based on ecological characters is not practical for plant-parasitic Tylenchida as most of them are either fungal or root parasites. Most of them are polyphagous and, even as advanced root parasites, they show very limited preference to a particular plant species. Mayr's (1969) definition of a genus is more practical to this group of animals, namely, 'A genus is a taxonomic category containing a single species, or a monophyletic group of species, which is separated from other taxa of the same rank (other genera) by a decided gap.' In nature, however, the decided gap between the genera narrows down as more species are discovered. Nevertheless, some distinguishing generic characters remain valid even in those genera which have a large number of species, e.g. the oesophageal glands forming a wraparound over the anterior end of the intestine with a greater extension on the ventral side in *Helicotylenchus*. However, in a related genus *Rotylenchus*,

which has the greatest extension of glands on the dorsal side of the intestine, the glandular overlap of the intestine varies from none (in subgenus *Pararotylenchus*) or slight (*R. breviglans*) to long (*R. robustus*). The proposal by Fortuner and Luc (1987) for having large-sized genera, e.g. *Filenchus* (including *Discotylenchus*, *Duosulcius*, *Ottolenchus* and *Zanenchus*) and *Tylenchorhynchus* (including *Bitylenchus*, *Mulkorhynchus*, *Quinisulcius* and *Telotylenchus*), has not met with general acceptance.

### (i) Morphological Taxonomy

Morphology continues to be the basis for the taxonomy and classification of Tylenchida. The above discussion of the morphological characters shows that there is a great deal of scope for their use in the determination of species, genera and higher categories and in deciding their placements into groups and systems. The morphospecies concept based on the separation of species on morphological characters, as against the biological or genetic species concept which defines species as interbreeding natural populations that are reproductively isolated from other such groups, will continue for these nematodes which, in many cases, are parthenogenetic. For Tylenchida, the biological species concept is difficult to apply since reproductive isolation cannot be demonstrated in uniparental species. Morphological differences are the main characters for species identification. In bisexual species, reproductively isolated populations which are similar in morphology may exist as different subspecies (*Radopholus similis similis* and *R. similis citrophilus*). R.P. Esser (personal communication, June, 1988) wrote: 'Alpha taxonomy is in desperate trouble around the world and it is vitally important that **all** taxonomists unite and support each other's efforts, lest we be submerged by shallow attempts at identification by so called sophisticated methods which are no more than cook-book exercises in futility. Alpha taxonomy is at present the basis for all research involving life forms. One must seriously question the basic correct speciation of species utilized in so called sophisticated modes of identifications.'

In using morphology in taxonomy, it is very important to know the range of variability in a particular character under different conditions. Morphometric, allometric and morphological characters tend to vary under the influence of geographical and ecological conditions which result in ecotypic and host-specific populations. Such populations are sometimes described as new species, although the differences between them are intraspecific variations.

### Variation and speciation

Living organisms and their surroundings are undergoing a continuous change. Comparative studies of animals are based on these changes occurring through time. The evolution and adaptive radiation of animals involve progressive changes in their morphology and biology. Ecological habitat and available plant and animal life exert immense pressure on survival, and the successful animals are those that have the ability to adjust and adapt to the changing habitat. Mutation and recombination in genetic material and geographical, genetic and physiological isolations often produce diversity of a particular species. Suitable habitats which can sustain large communities often modify animals of different structure and biology to look similar, thus resulting in convergent or parallel evolution.

The forces of natural selection act on the variations present in the populations

of animals and speciation may result when an ancestral species splits into two or more species which are different in morphology and are reproductively isolated from the parent and sister species. However, species may undergo changes and adaptations without splitting or branching. Evolution is not expected to be orthogenetic or unidirectional. The evolutionary events are often episodic and saltatory. Eldredge & Gould (1972) proposed that evolutionary changes take place as 'punctuated equilibria' in contrast to the phyletic gradualism. The speciation takes place in four steps according to the theory of punctuated equilibrium:

1. The species are in equilibrium with their biological and physical environment and continue to persist for a long time with almost no change.
2. Punctuations or sporadic events occur in geological time as speciation events.
3. New species originate in pocket(s) at the periphery of the range of distribution of the ancestral species.
4. Gradually the new species replace(s) the ancestral or parental species.

It seems that the mosaic pattern of evolution occurs over time, with unequal rates of development of various characters or features, together with the rudimentation or oligomerization of characters and their retrogressive modifications in the progeny of a parent species, which makes it difficult to understand the phylogenetic relationships of groups. Some animal species appear to change little over millions of years, while others transform considerably over a much shorter span of time. The species of Tylenchida are, and have been, undergoing evolutionary change. Populations of nematodes are constantly reacting to their environment and are subjected to various selection pressures. Meeuse (1979, 1982) stressed the significance of eco-physiological, eco-biochemical and eco-functional aspects of evolutionary processes on organisms. Cain (1982) writes, 'In the long term (except where the breeding system is affected) it is ecology, not genetics, that dictates the course of evolution.'

Stable changes in a species phenotype result from changes in its genome. Saltations are rare, but minor changes in genome may result in major changes in the phenotype. Uniparental, parthenogenetic species (e.g. *Helicotylenchus*, *Meloidogyne*) will probably experience greater changes in the gene pool through clone formation due to the lack of recombination and reorganization of the genetic material through amphimixis. In Tylenchida parthenogenesis is encountered in polyphagous genera which have a greater chance of finding food with ease. Parthenogenesis reflects a certain environmental stability, not requiring a high degree of genetic variability in the population (Poinar & Hansen, 1983).

Variations shown by a species are best studied by raising progenies of a single female and populations from different geographical areas should be studied for geographical variations. Great variations in morphometric and morphological characters of *Pratylenchus penetrans* were observed when populations were subjected to different environments (Tarte & Mai, 1976). Some characters used to differentiate species of *Pratylenchus*, e.g. stylet knob shape, length of outer margins of cephalic framework, the shapes of the spermatheca and tail, varied considerably. For example, when fed on pea roots, large numbers of females showed crenate tail tips (a character used to differentiate species of *Pratylenchus*) suggesting that hosts modify the phenotypical expression of tail type.

Parthenogenesis plays a major part in the speciation of polyphagous Tylenchida.

Triantaphyllou (1984) pointed out that polyploidy is common in mitotically parthenogenetic species of *Meloidogyne*. He speculated that *Meloidogyne* arose by polyploidization and subsequent diploidization of the genome by parthenogenesis. From then on, part of the genus returned to obligatory amphimixis, leading a more specialized parasitic life (e.g. *M. carolinensis*, *M. megatyla* and *M. microtyla*), while the remainder progressed by parthenogenesis to forms with extensive cytogenetic diversification, involving polyploidy and aneuploidy, and less intensive host specialization (e.g. *M. arenaria*, *M. incognita* and *M. javanica*).

The study of morphological characters has received great impetus by the use of scanning and transmission electron microscopes revealing details of surface and internal structures with unbelievable magnification and clarity. The scanning electron microscope (SEM) has even been used to study the morphology of internal structures, e.g. the stylet of *Meloidogyne* was shown to have different shapes in different species, characters which cannot be studied by light microscopy (Eisenback, 1982). However, for practical reasons, the characters revealed by SEM should not be the sole basis for taxonomic differentiation.

The study of face views of nematodes by scanning electron microscopy has solved several systematic problems. For example, the face view of *Pratylenchoides magnicauda*, which was previously assigned to *Tylenchorhynchus*, *Amplimerlinius* or *Hoplorhynchus*, resembles those of other species in the genus *Pratylenchoides* (Baldwin *et al.*, 1983). *Dolichodorus*, *Neodolichodorus* and *Brachydorus* can be differentiated by the amphidial apertures being longitudinal in *Dolichodorus*, round or dorso-ventrally directed in *Neodolichodorus* and obliquely placed in *Brachydorus*.

Since individuals and populations of a species may show considerable variation in morphological characters, it is important to study as many individuals as possible particularly from different hosts and geographical locations. These intraspecies variations may be intrinsic, due to genetic changes, extrinsic, due to external influences, or a combination of both. Since there is no recombination of genetic material, the parthenogenetic species show a wider range of intraspecies variations. An example is the genus *Helicotylenchus*, of which several new species have been proposed on minor differences in morphological characters.

Techniques, type of equipment, methods of observation and personal skills may also lead to morphometric variations. Measurements made by 14 taxonomists in seven countries on one female specimen of *Pratylenchus coffeae* produced great variations in body measurements and morphometric ratios (Frederick & Tarjan, 1978). Hence morphometric and allometric differences should not be the main criteria for species differentiation, although they may be supplementary to the morphological characters. Thorne & Malek (1968) thought a 10% variation in such characters to be of little taxonomic value and preferred to give means rather than ranges of measurements. However, it is always useful to give ranges as well as means of measurements of a particular population to serve as a record.

Populations derived from a single egg or female studied under the influence of different environmental factors, such as temperature, moisture, soil type and host plant, show a wide range of variation particularly in biometrical characters. Such populations could be described as new species by those who do not take into consideration the variability shown by morphological and morphometrical characters. Coomans (1963) found much variation in the number of cephalic annules and the

subdivision of the basal annule in *Hoplolaimus pararobustus*, but new species based on these characters have been proposed recently. *Criconemoides informis* and *Macroposthonia xenoplax* populations with males had fewer numbers of total body annules than those lacking males and there was an indication that populations from the temperate zones had a longer stylet than those from tropical areas (De Grisse & Loof, 1970).

Of 20 morphometric characters studied in populations of *Pratylenchus* by Roman & Hirschmann (1969), vulva position (V value) and stylet length were found to be stable, but the lateral field incisures, number of annules in the cephalic region and the shapes of stylet knobs and tail varied considerably. In populations of *Helicotylenchus indicus*, Azmi & Jairajpuri (1978) found that the position of the vulva and nerve ring from the anterior end of the body and the length of the stylet were least variable and may serve as good diagnostic characters and that, among the allometric adult characters, V, a, and O ratios were also stable.

Zancada *et al.* (1988) used principal component analysis to assess 21 morphological/morphometrical characters in species differentiation of *Rotylenchus*. They proposed two new ratios, i.e.  $k$  = width of stylet knobs divided by height of stylet knobs, as an index of flatness of knobs, and the ratio  $rb$  = length of median bulb divided by width of median bulb, as an index of roundness of median bulb. They found the actual value of the distance from the orifice of the dorsal oesophageal gland to the stylet base as more significant than the ratio O.

The importance of bivariate or multivariate character analysis is now being stressed for the identification of species and genera. In a study of four populations of *Belonolaimus longicaudatus*, Rau & Fassuliotis (1970) found that mean stylet lengths were relatively stable compared with mean tail lengths and that, in forms with short stylets, stylet length was much more variable than in forms with long stylets.

A 95% **equal-frequency ellipse** can be plotted for measurements of normally distributed bivariate characters (stylet and tail length) and used to determine whether other populations are significantly different from this model. Such methods not only are useful in determining the graphic representation of morphological relationships within populations but also are of value in making comparisons with other species and in determining the effects of environmental and genetic changes on population morphology. For example, the use of ellipses formed from the bivariate measurements of the distance from the head end to the median oesophageal bulb and the total body length helped to distinguish between juveniles of *Meloidogyne javanica* and *M. incognita acrita*, while mixed populations of *Pratylenchus brachyurus* and *P. zeae* were readily separated when the characters distance from the head end to vulva or anus and total body length were used (Rau & Fassuliotis, 1970).

**Microcomputers** (personal computers) with advanced speed and power provide a very useful tool for the identification and systematics of nematodes. Computer-aided semi-automatic identification schemes are being developed for some Tylenchida which show a high variability of morphological characters (Boag, 1981; Fortuner, 1983, 1989; Boag *et al.*, 1989). Dichotomous keys to genera with a large number of species (e.g. key to *Helicotylenchus* by Siddiqi, 1972) soon become unmanageable and outdated when more species are added. Computer programs are designed to manage the large quantity of taxonomic data conveniently and

efficiently. Such programs should be standardized and user-friendly, relatively inexpensive and widely available.

Where a large number of taxa are to be compared and masses of data are to be handled, computer programs become necessary. The problems involved in obtaining the most stringent comparisons between taxa include choosing characters and applying a similarity index to them. Fortuner (1983) and Fortuner & Wong (1984) used a large mainframe computer to produce a sophisticated program NEMAID for the identification of *Helicotylenchus* spp. based on Gower's (1971) coefficient of similarity. This program was made available on floppy disks to be used by microcomputers and through the TELENET system (Fortuner, 1986).

Identification (generic and specific) methods using computer programs are called expert-systems, which are part of man-made artificial intelligence. An expert-system called NEMISYS was created with the help and collaboration of more than 30 nematologists for the identification of Tylenchida. Concepts of promorph and nest were developed to allow practical identification. The promorphs are forms recognized under low magnification with primary differentiating criteria but without detailed morphological identification. Similar promorphs are grouped under one nest; promorphs and nests do not represent species and genera, respectively (see Fortuner, 1989, and Diederich *et al.*, 1989 and 2000, for details of NEMISYS).

Rey *et al.* (1989) transformed qualitative characters into quantitative characters by giving binary (presence or absence) and quantitative continuous characters as real numbers, quantitative discontinuous characters as integers and qualitative multivariate characters coded on a scale from 1 to 4, and, for the similarity index, the general coefficient of similarity of Gower (1971) and the index of Pinkham & Pearson (1976) were used, with a correction factor for missing values. They developed a computer simulation model to study the efficiency of quantification of qualitative characters, the weighting and also the correction factor applied, and the comparison of the indices of similarity of Gower and of Pinkham & Pearson.

Hasan (1990) stated: 'Since the very purpose of taxonomy is to evolve a system which may enable even to the non-experts to identify various species correctly which is the dire need of the extension/field workers, breeders and others who are concerned with nature and its diversity. Even at this stage, stability in taxonomy to some extent, can be enforced but through the sound judgement of the worker who may exercise it if he is properly trained, has strong reasoning power, is not prejudiced to allied practices like numerical, experimental taxonomy etc.' However, the use of computer-assisted identification of nematodes by non-taxonomists was strongly supported by Diederich *et al.* (2000) who wrote: 'Only computer identification tools are flexible, reliable, and general enough to give a non-taxonomist the possibility to identify any species.'

## (ii) Physiological, Biochemical and Cytogenetic Taxonomy

Host response to parasitism may provide differentiating characters. For example, Heteroderinae induces two basic responses (which are not host-dependent but represent the characteristic nature of the digestive enzymes of the nematode) in the production of nurse cells: the single uninucleate giant cell (found in *Meloidodera* and *Sarisoderini*) and the multinucleate syncytium found in members of *Heteroderini* and *Ataloderini*. The syncytia differ in size and in having wall ingrowths. *Ekphymatodera*

*thomasoni* induces a syncytium which is much smaller than that of Heteroderini (except *Punctodera*) or Ataloderini and the absence of wall ingrowths is shared by *Atalodera* and *Afenestrata* (Mundo-Ocampo & Baldwin, 1992). The uninucleate giant cell response of the host appears to be a primitive character and the syncytium response a derived one. The two types of syncytium, with ingrowths in Heteroderinae and without ingrowths in Ataloderinae, are supposed to be fundamentally different and might have been the result of parallel evolution (Baldwin, 1986). Females, eggs and juveniles of *Trophotylenchulus* are enclosed in a brittle capsule-like structure, probably produced by the host, but such a host reaction is absent in *Tylenchulus*.

The study of the karyotype including chromosome number and morphology and the mode of reproduction has provided valuable information on the taxonomy and systematics of Heteroderidae and Meloidogynidae. Triantaphyllou (1970) examined the variation in the basic karyotype of the Heteroderidae, including the establishment of polyploidy and aneuploidy, to trace the pathways of evolution of this group. For example, *Heterodera galeopsidis*, *H. lespedezae* and *H. trifolii*, which reproduce by mitotic parthenogenesis and have somatic chromosome numbers from 24 to 34, appear to have been derived from forms such as *H. schachtii* and *H. glycines*, to which they are morphologically related, through various chromosomal changes along the same phyletic line or several parallel lines derived from the same basic species. These species represent a parthenogenetic complex, genetically isolated from the amphimictic species (e.g. *H. schachtii*, *H. glycines*, *H. avenae*, etc.) from which they may have been derived.

Triantaphyllou (1983) observed a correlation between the evolution of higher plant-parasitic nematodes (namely, their advanced parasitic specialization) and the increase in chromosome number and in the amount of deoxyribonucleic acid (DNA), as well as the establishment of parthenogenetic reproduction. The basic chromosome number ranges from  $n = 1$  in free-living *Diploscapter coronatus* to  $n = 19$  in seed-parasitic *Anguina tritici*; larger chromosome numbers result from polyploidy (e.g.  $3n = 54$  in *Meloidogynae arenaria*). Chromosome numbers studied in Tylenchida summarized by Triantaphyllou are shown in Table 3.

Unlike other orders of Secernentea, parthenogenesis occurs widely in Tylenchida and seems to have been established independently in many lines of evolution of these nematodes (Triantaphyllou, 1983).

**Table 3.** Chromosome numbers in Tylenchida.

Taxon	Chromosome number
Criconematoidea:	$n = 5$
Anguinoidea: <i>Anguina</i> :	$n = 9$ (polyploids 18, 27), 12
<i>Ditylenchus</i> :	$n = 12$ (polyploid 24)
Dolichodoridae:	$n = 8$
Belonolaimidae:	$n = 8$
Pratylenchidae:	$n = 5-7$ (polyploids 10-16)
Hoplolaimidae:	$n = 5$ (polyploid 10), 8
Meloidogynidae:	$n = 18$ (polyploids 36, 54), 14-17
Heteroderidae:	$n = 9$ (polyploid 18), 12-13

Source: Triantaphyllou (1983).



Polyploidy commonly occurs in mitotically parthenogenetic species of *Meloidogyne*, e.g. *M. hapla*. *Meloidogyne hapla* race A has somatic chromosome numbers 28 to 34 ( $n = 14-17$ ), while race B either has  $2n = 30-32$  (diploid) or  $2n = 45-48$  (triploid) (Triantaphyllou, 1966). In polyploid meiotic forms, in the presence of males, it is assumed, polyploid amphimixis could have been established. Triantaphyllou (1983) supposes that this type of mechanism could have led to the establishment of *Meloidogyne* species with  $n = 18$  chromosomes, which indeed are polyploids descended from ancestors with about half as many chromosomes (cf. Heteroderidae  $n = 9$ ). The existence of *Spartonema spartinae* with  $n = 7$  chromosomes supports this assumption.

Cytogenetic analysis can be used in species or pathotype differentiation. Hackney (1974) developed a useful scheme for the identification of *Meloidogyne* spp. on grapes using chromosome number supplemented with perineal pattern and juvenile measurements. On perineal pattern alone, most nematodes, except *M. javanica*, were identified as *M. arenaria*, but the chromosome numbers of 43, 47, 42, 37, 52 and 17 indicated the presence respectively, of *M. javanica* (or *M. incognita*), *M. javanica*, *M. incognita*, *M. arenaria* ( $2n$  form), *M. arenaria* ( $3n$  form), and *M. hapla* race A; *M. javanica* and *M. incognita* were separated from each other using perineal pattern.

Biochemical techniques of protein analysis are now increasingly used to separate pathotypes and species of Heteroderidae and Meloidogynidae. Monoxenic cultures of Tylenchida on plant callus tissue and mycelia may greatly help in providing large quantities of nematodes for these purposes. Immunological techniques, DNA hybridization and isoenzyme analysis are now being applied to the Tylenchida taxonomy. The potential of these techniques and analyses in nematode identification and for the unravelling of phylogenetic relationships is enormous. Special biochemical knowledge, skills and instrumentation are, however, a prerequisite for such sophisticated techniques.

Hussey (1979) reviewed the work done on biochemical systematics of free-living and plant-parasitic nematodes. Gel electrophoresis is by far the most widely used technique because it is simple (see Gordon, 1970; Mauerer, 1971) and gives quick results in protein and enzyme characterization. However, Hussey (1979) warns that the number of protein bands and isoenzymes (that are detected) and their electrophoretic mobility may be seriously affected by methods of culturing nematodes (due to host effect), stage of nematode development, protein extraction procedure, condition of storage of extracted protein and methods of protein and enzyme analysis.

Evans (1971) was able to distinguish between populations of *Ditylenchus destructor* and *D. myceliophagus* on the basis of their esterase patterns as revealed by gel electrophoresis. Dickson *et al.* (1970) obtained different protein band profiles by using disc electrophoretic separation of soluble proteins of some selected species of *Ditylenchus*, *Heterodera* and *Meloidogyne*. Certain protein bands were common to all the species of *Meloidogyne*, but there were others which were specific and of taxonomic value. Protein profiles of populations of the same species from different geographical regions and different hosts were similar.

Gel electrophoresis coupled with enzyme-specific staining is useful in identification and taxonomy. The sensitivity of gel electrophoresis is enhanced when used

along with techniques for the identification of specific enzymes. Two-dimensional electrophoresis, combined with a sensitive protein stain based on a reaction with silver ions, was used to differentiate *Globodera pallida* from *G. rostochiensis* (Bakker & Gommers, 1982). A very small quantity of protein (25 µg) was needed for this test. A single protein difference characterized pathotypes RO<sub>1</sub> and RO<sub>5</sub> of *G. rostochiensis*.

Using two-dimensional polyacrylamide gel electrophoresis, protein patterns are studied for interspecies comparisons. Morphologically, *Globodera pallida* is very similar to *G. rostochiensis*, but the two species were discriminated by 70% of their polypeptides resolved by two-dimensional gel electrophoresis. This difference is more than that between humans and orang-utans using this assay (see Gheysen & van Montagu, 1995). A study using two-dimensional gel electrophoresis showed that *Globodera virginiae*, *G. solanacearum* and *G. tabacum* can be regarded as only one species, *G. tabacum sensu lato*, and that *G. mexicana* is closer to *G. pallida* than *G. rostochiensis* (Bossis & Mugniéry, 1993).

Modern techniques have greatly improved detection, identification and estimation of populations in the field samples. Dickson *et al.* (1971), using disc-electrophoretic analysis of specific enzymes, demonstrated the interrelationships of some *Meloidogyne* species. *Meloidogyne javanica* and *M. arenaria* are more closely related to *M. incognita* than any of them are to *M. hapla*. *Meloidogyne hapla* has the greatest number of non-matching enzyme bands, which means it may be a more primitive form that diverged from other species at an early date. Two lineages, one giving rise to *M. hapla* and the other to *M. arenaria*, *M. incognita* and *M. javanica*, are thus indicated. Further studies, based on many more species and populations, are, however, needed to construct a reliable phylogeny of *Meloidogyne* or of any other member of the Tylenchida.

Polyacrylamide gel electrophoresis (**PAGE**) has been used for separating enzymes and protein profiles to characterize interspecific variations, aid in pathotype and species identifications and compare evolutionary divergence among nematodes. Among others, enzyme esterase analysis has proved to be reliable in distinguishing species, particularly those which are similar in morphological characters. It has served as an effective method in comparing species of *Heterodera*, *Meloidogyne* and *Ditylenchus*.

Esbenshade & Triantaphyllou (1985) used enzyme phenotypes, such as esterases, malate dehydrogenase, superoxide dismutase and glutamate oxaloacetate transaminase, for the differentiation between *Meloidogyne* species. Ibrahim and Rowe (1995) analysed non-specific esterase phenotypes of 19 species of *Heterodera* with isoelectric focusing and found them to belong to six species groups according to the clustering and percentage distance between the clusters of esterase banding patterns.

Modern techniques in the field of biotechnology have greatly improved detection and estimation of populations in field samples. Species are identified using monoclonal antibodies (**MAbs**) which recognize species-specific proteins in adults, juveniles or eggs in an enzyme-linked immunosorbent assay (**ELISA**). Nematode protein is extracted and injected subcutaneously into rabbits or mice which develop antibodies. Antisera containing antibodies are then obtained from the blood and when mixed with antigen (nematode protein) show antigen-antibody reaction. The band patterns of this reaction are analysed by ELISA and matched.

MAbs, with quantification by ELISA, have been developed and used for differ-

entiating root-knot and cyst nematodes. Schots *et al.* (1992) described a quantitative ELISA method for the detection in the soil of *G. rostochiensis* and a related species *G. pallida*. Suitable MABs which are typified by uniform physical characteristics are developed using the hybridoma technique of Köhler and Milstein (1975). Once the major antigen-antibody binding parameters have been determined, the behaviour of MABs in an immunoassay can be predicted for the qualitative and quantitative determination of species.

Biotechnology is increasingly being applied in systematics involving the quantification and identification of specific genes by nuclei hybridization. Where changes in phenotype are difficult to detect, DNA provides a useful tool for differentiating recently diverged taxa at species/subspecies or even pathotype/race level. Study of the nematode genome at the molecular level using nucleotide sequencing has revealed morphological, cytogenetic and biological diversity which helps in the identification and phylogenetic work. DNA fragmentation patterns are repeated thousands of times in chromosomes and show variation between species. A single-copy DNA segment obtained by molecular cloning can serve as a probe which can bind to any similar single-strand molecule with which it shares nucleotide sequence complementarity.

It is very important in economic nematology to distinguish between plant-damaging (virulent) and non-damaging (non-virulent) species/subspecies/populations. DNA hybridization probes or markers are used for detecting target species in samples of populations. The ultimate genomic mapping of plant-parasitic nematodes will not only help in differentiating closely related species and identifying races, but will also help in solving many biological problems, understanding co-evolutionary trends and developing phylogenetic relationships. Within the last 10 years, a variety of DNA-based techniques have been so much developed and used in identification and taxonomy of plant and entomophilic nematodes, particularly *Heterodera*, *Meloidogyne*, *Bursaphelenchus* and *Steinernema*, as to be classified as a separate discipline (see Gheysen & van Montagu, 1995). DNA fingerprinting techniques use restriction enzymes for cutting complex genomic DNA into many differently sized fragments, which provide differential information when separated by electrophoresis. Restriction enzyme recognition in polymerized variable fragments of DNA is obtained by restriction fragment length polymorphism (**RFLP**) to characterize various populations, isolates or species of nematodes. Data obtained on the presence or absence of polymorphism and on the intensities of corresponding DNA fragments are analysed and dendrograms constructed. Such DNA-based techniques have several advantages over morphological and biochemical taxonomic methods:

1. The amount of DNA sequence polymorphism obtained by hybridization is enormous and large numbers of specimens are not needed to study the degree of phenetic variation or phylogenetic divergence.
2. Most DNA markers are not affected by changes in the environmental conditions or developmental stages of nematodes.
3. Most changes in DNA have little effect on the protein and hence are almost free from selection pressures.
4. The percentage similarity in a DNA sequence is stable as a marker for a phylogenetic relationship.

Technologies based on the study of recombinant DNA and restriction fragment length polymorphism can afford a simple and accurate methodology for species and biotype differentiation. The technique uses restriction enzymes to generate fragments of DNA to be separated and studied by gel electrophoresis. Different banding patterns are seen where alterations in fragment sizes of the DNA sequence have occurred. These restriction fragments from the total DNA digest are detected as recognizable bands by electrophoresis on agarose gel. The RFLPs have been obtained by digestion of total DNA with restriction endonucleases which recognize specific nucleic acid sequences in DNA and cleave the DNA molecules at specific sites, and these are mapped to differentiating characters for comparison between races and species.

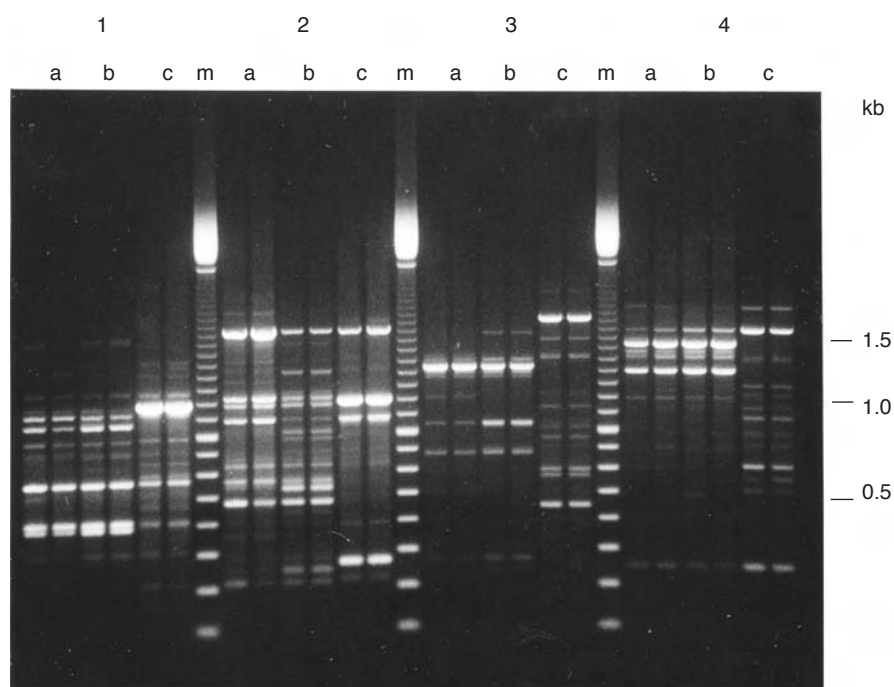
Genomic regions exhibiting DNA polymorphisms have been detected in many plant-parasitic nematodes. Among *Meloidogyne* populations, RFLP variability is easily detected in both repetitive and low-copy nuclear sequences. Although large amounts of nematodes are needed and not much information is available on inter-population variability of known gene coding sequences, there is great potential in RFLP study for knowing the degree of divergence between repeated DNA polymorphisms (exemplified by hybridization), which should help in the understanding of the time taken in the evolution of species. Low-copy-number sequences can be used as probes on restriction-digested DNA samples, utilizing various restriction enzymes with each probe. Clones that contain moderately repeated sequences are generally used as probes. A cloned ribosomal DNA (**rDNA**) fragment isolated from *Caenorhabditis elegans* is used as a probe to differentiate between species and races of *Meloidogyne*. The genome of *Globodera pallida* was estimated to contain  $1 \times 10^8$  base pairs, which was not significantly different from the genome size of *Caenorhabditis elegans* when estimated by direct microdensitometry of stained somatic nuclei (Grisi *et al.*, 1995).

Application of DNA hybridization probes to nematode total genomic DNA in the eggs of *M. incognita* race 3, *M. arenaria* race 1 and *M. javanica* revealed RFLPs which showed that *M. arenaria* and *M. javanica* are more closely related to each other than they are to *M. incognita*. The phylogenetic tree of the three species as generated from the hybridization data gave an estimate of their divergence time from a common ancestor of 2–4 million years (Xue *et al.*, 1992). Zijlstra *et al.* (1997) devised a method based on ITS (internally transcribed spacer)-RFLPs to differentiate individual species of *Meloidogyne* species in mixtures (of *M. incognita*, *M. hapla*, *M. chitwoodi* and *M. fallax*).

DNA-based diagnostics received a boost with the development of the polymerase chain reaction (**PCR**) as a tool for differentiation between species. DNA from nematodes is obtained by crushing them in sterile water and then adding the suspension to the PCR mix. The PCR conditions and mix components are varied to obtain clear and reproducible banding patterns. In PCR and DNA sequencing, a DNA template is amplified by polymerization reaction using a DNA polymerase enzyme and an oligonucleotide primer. Single oligonucleotide primers are identified which give distinct molecular fingerprints for various species of a genus. The random amplified polymorphic DNA (**RAPD**) fingerprinting technique is now widely used because substantial data can be generated in a short time and no DNA sequence information is needed. Originally, it was used as DNA markers to con-

struct genetic maps for different organisms including man and soybean (Williams *et al.*, 1990), but recently several nematologists have been using it for distinguishing between species. RAPD profiles can serve as diagnostic molecular characters at different taxonomic levels. Studying the genetic variation in tropical *Meloidogyne* spp. using DNA (RAPD), Blok *et al.* (1997) found three virulent lines of *M. arenaria* which could be differentiated from an avirulent line of this species and other lines of *M. javanica*, *M. incognita*, *M. hapla* and *M. mayaguensis*.

Siddiqi and Hahn (1995) studied the genomic divergence of a population of *Radopholus bridgei* Siddiqi & Hahn, 1995 from populations of *R. similis* (Fig. 12). The genomic DNA of *R. bridgei* was found to be very divergent from that of 14 *R. similis* and two *R. similis citrophilus* populations. A comparison of ribosomal DNA sequencing involving spacers and small portions of gene loci is made to study inter-relationships between species. Fallas *et al.* (1996) studied 11 isolates of *R. similis* from various banana-growing regions in the world and one isolate of *R. bridgei* from turmeric in Indonesia. Data obtained by RAPD analysis of total DNA and subjected to hierarchical analysis arranged the *R. similis* isolates into two clusters – one of the isolates from Nigeria, Cameroon, Queensland and Costa Rica, the other of isolates



**Fig. 12.** Random amplified polymorphic DNA profiles from two populations of *Radopholus similis* and one population of *Radopholus bridgei*. Profiles were generated by primers OPA-03 (1), OPA-09 (2), OPE-09 (3) and OPK-02 (4) from genomic DNA of *R. similis* from banana in Kenya (a), *R. similis* from tea in Sri Lanka (b) and *R. bridgei* from turmeric in Indonesia (c). Molecular size values given in kilobases (kb) were estimated from 100 bp ladder (m). (After Siddiqi & Hahn (1995), courtesy *International Journal of Nematology*.)

from Guinea, Guadeloupe, Côte d'Ivoire, Uganda and Sri Lanka; the isolate of *R. bridgei* appeared to be more divergent.

Molecular biologists, realizing the simple genetic constitution of the mitochondrial genome and its relevance to population and evolutionary biology, worked on *Caenorhabditis elegans* as a biological tool. The characterization by restriction enzyme analysis of double-stranded mitochondrial DNA (**mtDNA**), which comprises of 1–10% of a eukaryotic cell, was soon applied to the plant-parasitic Tylenchida, mainly to characterize populations, pathotypes and species. Restriction fragment length polymorphisms within mtDNA are easily visualized by gel electrophoresis and provide convenient markers for identification of races, pathotypes and species.

Mitochondrial DNA, a small extranuclear genome, provides a genetic marker for a rapid and reliable method to differentiate between species and races of nematodes. It is present in hundreds of copies within each cell. It is very useful in phylogenetic studies because, being inherited maternally, it is free from genetic recombination, it shows a rapid rate of evolution with less variation in gene content, and its RFLP can be analysed directly without hybridization. A high rate of mtDNA evolution and its high cellular copy number allow a quick comparison between species. mtDNA is isolated from nematode and egg lysates and then digested with different restriction enzymes. mtDNA sequencing has been extensively studied for *Caenorhabditis elegans*. It is now being used for comparing species and races of *Meloidogyne* using RFLP.

DNA, rDNA and mtDNA sequencing also provides a powerful tool for studying phylogenetic relationships of nematodes. Species relationships can be studied from the combination of nuclear, mitochondrial and enzymatic data. A comparison of mtDNA from the sibling species *Heterodera glycines* and *H. schachtii* showed that they diverged from a common ancestor 7.3–14.8 million years ago (Radice *et al.*, 1988). Miller (1976) had successfully interbred these two species which show some morphological differences and have separate geographical distributions.

DNA probes of cloned fragments of DNA with about 370 base pairs were isolated from *G. pallida* second-stage juveniles and used to differentiate between *Globodera pallida* and *G. rostochiensis*. The cloned genomic DNA hybridized strongly with DNA from populations of *G. pallida* but not from those of *G. rostochiensis*. Stressing the importance of DNA probes in differentiating nematode species, Burrows & Perry (1988) wrote: 'Recent studies in genomic evolution indicate that frequent and rapid changes in repetitive DNA may be involved in speciation (MacGregor, 1982). Tandem and dispersed repeated DNA families have demonstrated a high degree of homogeneity within species with much greater variation between species. This phenomenon, known as **concerted evolution**, has been well documented but it is difficult to explain in terms of natural selection or drift (Dover *et al.*, 1982). The observed homogeneity in repeated DNA families between species enhances their potential for differentiating nematode species.'

In deriving phylogenetic relationships from nucleotide sequences, Ferris (1994) stated that considerable investigation is necessary to determine an appropriate DNA or RNA region on which to rely for a particular group at a given taxonomic level. She cautioned, 'The kind of cluster analysis based on total similarity that is often used with molecular data, would place the cyst nematodes closer to *Xenopus* than to

*C. elegans* if used with our 5.8S ribosomal gene data. This would be nonsense if interpreted in terms of species relationships.'

### (iii) Evolutionary Systematics

The traditional evolutionary approach involves the reconstruction of the phylogeny using data obtained from fossils and comparative morphology. This is the strato-phenetic approach, linking the past with the present by building **ancestor–descendant sequences** and presenting their data as **genealogical trees** (Simpson, 1961; Mayr, 1969).

Present-day species are supposed to have evolved by successive adaptations and modifications from species having primitive and simplified characters or character states. The groups are supposed to be connected by intermediate links which are often hypothetical. Crowson (1982), however, points out that the ancestral species need not be simplified and generalized forms since they 'must have been capable of survival as members of more or less complex and competitive ecosystems'.

**Fossils** of past animals provide markers in the tracing of evolution and help in understanding what the state of organisms actually was in the past. Unfortunately, Tylenchida has only two fossil records – a Hexatylinia parasitizing a drosophilid fly and a fungus gnat fossilized in Dominican amber about 25 million years ago, as reported by Poinar (1984, 1991). Around the fly were 120 juvenile nematodes which had emerged from its abdomen after it had ruptured in the amber. The nematodes (0.14–0.24 mm long, 6–8  $\mu\text{m}$  wide) appeared to be third- and fourth-stage juveniles and Poinar (1984) believes that the finding shows that these 'allantonematids' were well established as groups in the Mid-Tertiary, and that their origin extended well before that period. The finding of these fossils, however, does not help much in the taxonomy or classification of the Tylenchida.

Even if a large number of fossils of Tylenchida were known and available to the taxonomists, there would hardly be any meaningful advantage in drawing phylogenetic conclusions from them. Forey (1982) writes, 'In fact, I do not think it unfair to say that fossils, or at least the traditional interpretation of fossils, have clouded rather than clarified our attempts to reconstruct phylogeny.' So, the phylogeny is largely hypothetical and a matter for conjecture and speculation based on the present-day forms.

The **semaphoront**, an organism at a given time constituting a complex of characters, is the operational taxonomic unit which is open to phylogenetic interpretation (Hennig, 1966; Rieppel, 1980). The reconstruction of phylogeny should be carried out by tracing the likely pathways of ancestral characters, although it is an impossible task to **establish** the course of evolution.

Firstly, the ancestral (primitive) characters are to be determined and, secondly, their relative stability during transformation is to be studied, the latter involving determination of derived (acquired) characters as well. If, for example, species A evolved to B and C, then B and C are expected to have most of the characters of A, but they are also expected to have additional (i.e. derived) characters which would distinguish B and C. The entire exercise depends on determining **homologies in ancestral characters** in terms of evolution.

**Homology** (Greek *homoios* = same, *logos* = discourse) is resemblance due to inheritance from a common ancestor (Simpson, 1961). Homologies are traced and

verified if they are ancestral or a part of transformational stages of an ancestral character. In contrast, **analogy** (Greek *ana* = again, up to) or **homoplasy** (Greek *plasis* = moulding) is resemblance due to parallel evolution or convergence. **Parallelism** is the development of similar characters or character states arising in separate lineages of common ancestry and **convergence** results in similar characters in separate lineages involving a common function through common adaptation. According to Mayr (1969), 'Features (or states of features) are **homologous** in two or more organisms if they can be traced back to the same feature (or state) in the common ancestor of these organisms', while, following Hennig (1966), homologous characters are '**transformation stages** of the same original character'. Ghiselin (1976) regards homologues as structures that arise from the same source, being of two types: (i) **iterative**, incorporating serial, sexual and antimeric (right and left symmetrical halves of body); and (ii) **evolutionary** or phylogenetic.

Roth (1984) gives a modified definition to enable reconstruction of the hierarchies and to recognize the varying degrees of strengths of homology, by saying: 'The basis of homology in the broad sense is the sharing of pathways of development, which are controlled by geneologically-related genes.' The developmental pathways are regulated by a particular battery of genes, or genes duplicated within an individual, or genes that bear a sister-group relationship to one another. This definition is more representative of **genetic homology**. **Biochemical homology** deals with various types of correspondences which can be detected at the molecular level, including those between steps in synthetic pathways. **Behavioural homology** is also important in phylogenetic reconstruction, and perhaps more difficult to determine than the other types of homologies.

**Taxonomic homologies** (= homologies used to characterize hierarchic groupings) can, according to Patterson (1982), be **tested** in three ways: (i) by **conjunction** (if homologues occur together in the same organism, the homology is rejected); (ii) by **similarity** (in composition, topography and ontogeny); and (iii) by **congruence** with other homologies (when two sets of homologies are incongruent, both can be shown to be improbable, and only one can be true). Similarly, for recognizing homoplasy (non-homology) these three tests can be used. If the homology fails in the conjunction test, it is due to **homonymy** and, if it fails in similarity (presence vs. absence), it is due to **complementarity**. However, if it fails in congruence, the result is due to parallelism. Hence, only the homologies that pass the congruence test are reliable in systematics.

#### (iv) Cladism

The cladistic approach to classification or phylogeny is known universally through Hennig's book *Phylogenetic Systematics*, which was published in 1966. Cladistic analysis is a kind of interpretation of similarities in and between taxa. The similarities are established by ingroup and outgroup comparison of two types of characters or character states. **Plesiomorphs** or ancestral characters or character states are more widely distributed and are studied in both ingroup and outgroup(s) comparisons while the **apomorphs** or derived characters are used in ingroup comparisons only. More precisely, cladism uses correspondence in shared characters or character states, which in the case of plesiomorphs is known as **symplesiomorphy**, and for apomorphs, as **synapomorphy**. The **commonality principle** states that plesiomorphs



will be commoner on average than apomorphs. This principle is probabilistic rather than deterministic in nature.

Cladism aims at determining the monophyletic and polyphyletic natures of synapomorphies. There are three types of **phyletic groups**. A group showing monophyly is called **monophyletic** and is comprised of all the descendants of an ancestor. It is characterized by synapomorphies (shared derived characters). A group based on analogous characters due to the occurrence of convergent or parallel evolution is a **polyphyletic** group; the group based on symplesiomorphies is referred to as **para-phyletic** (Platnick, 1977). Coomans (1983, p. 2) writes: 'monophyletic taxa have a common ancestor not found in common with any other taxon. Such an ancestor is a species; supraspecific taxa cannot be direct ancestors.'

It is important that synapomorphies are studied in one **transformation series** or **morphocline** and should not be confused with those in other series which may be due to convergence. For example, the position of the excretory pore anterior to the median bulb in mature females of *Meloidogyne* and *Meloinema* spp. is a synapomorphy in the transformation series of the family Meloidogynidae. It shows a closer phylogenetic similarity between the members of the two genera than between these genera and genera of the Heteroderidae, which share many synapomorphies with them (terminal vulva, absence of bursa, etc.), but represent a different transformation series, the family Heteroderidae.

**Polarity** refers to the evolutionary line of a character state transition. If the character state was found in the immediate common ancestor, it is plesiomorphic or primitive, if not, it is apomorphic or derived. In assessing character states, their polarity must be determined in order to understand the character transformation and their occurrences. This is done by comparative and ontogenetic methods (see Arnold, 1981).

**Comparative methods** are based on **ingroup** (members in the same monophyletic group or **clade**) and **outgroup** comparisons of homologies. Of the ingroup comparison, Jefferies (1979, p. 451) writes, 'If a homologous feature is universal in a monophyletic group, then it will have been present in the latest common ancestor of the group (e.g. hairs in mammals)' and for the outgroup comparison, he (p. 452) adds, 'If a feature is present among many relatives of a monophyletic group, and if its homologue occurs, sometimes or universally, in the members of the monophyletic groups, it will have been primitive for the group.' Patterson (1982, p. 52) is sceptical of these definitions since they are based on the assumption that monophyletic groups are already established and the loss or suppression of a feature within the group is not accounted for. He therefore accommodates for this by saying, 'If a homologous feature is universal in a group, then the group will be monophyletic, unless the feature is lost or suppressed within the group.'

The **ontogenetic method** of comparing homologies is based on Haeckel's law of recapitulation (the biogenetic law): ontogeny repeats phylogeny. The presence of spined annules in juveniles of smooth-annulated adults of *Hemicriconemoides* clearly shows that the ancestor of the genus had spined annules. But in the members of the Criconematinae, spined annules are characteristic of the adult females as well as of juveniles, and so are ancestral in character. Nelson (1978) pointed out that an ontogenetic character state which is more widely distributed among the members of a group than other states is likely to be primitive as the adult condition.

Coomans (1983, p. 5) states, 'adult character states often appear prior to others during ontogeny, and that in the case of progenesis and neoteny, the later stages of the ontogenetic series are lost or so much modified that they are no longer recognizable'. He believes comparing with outgroups and using additional characters should facilitate the recognition of progenesis and neoteny. There are characters in nematode juveniles that disappear in the adult state, as with the spined cuticle of the juvenile of *Hemicriconemoides*.

**Weighting** of a character or character state is the evaluation in terms of its phyletic information and its probable contribution to a sound classification which has most predictive value. For ingroup comparisons, synapomorphies (shared derived character states) are tested for reliability through weighting by various methods (see Arnold, 1981). Complex synapomorphies are more reliable because, during the course of evolution, the chances of their duplication would be minimal. Therefore, characters relating to genitalia (spicule, gubernaculum, hypopygium, epiptygma, vulva shape and position, etc.) could be taken as having more weighting than others because, due to reproductive isolation, they are different between groups, and for breeding they should remain stable between the two sexes (Coomans, 1983).

Once the lower-rank taxa are determined by establishing synapomorphies, they are then arranged in a dichotomous branching pattern – the **cladogram** or dendrogram. The splits or nodes in a cladogram represent points of diversification or phyletic sequences, although evolution is generally not spontaneous or saltatory, as may appear from the cladograms.

It may also appear from the branching pattern of a cladogram that the parent group expires when it gives rise to two daughter groups (= sister groups of Hennig). Mayr (1969) argues that this rarely happens in phylogeny because a new group buds off from a parent group and the latter continues to coexist with very little change for perhaps more than 100 million years.

Cladistic systematics deals with arranging the taxa in a hierarchical system by utilizing cladograms. However, several types and kinds of cladograms can be obtained by using different sets of characters and different conjectures of phylogenetic relationships. In such cases, the **rule of parsimony** (*parsimonia* literally meaning strict economy) is applied. Such cladograms which require fewest character state transitions or the least number of evolutionary steps are called the most parsimonious ones. Parsimony analysis employs methods to find the most parsimonious cladograms after discarding cladograms based on less reliable or weaker sets of characters (Cracraft, 1974). Only the most parsimonious cladograms that pass the rule of parsimony and have greater predictive value should form the basis for classification (Rieppel, 1979, 1980).

Several **algorithms** or systems for repeat analysis to get the best fit have been devised to find the shortest or most parsimonious cladogram. These are collectively referred to as **heuristic** methods (see details in Quicke, 1993).

Characters whose state distribution among taxa reflects or seems to reflect the evolutionary history and which represent variations due to phylogeny are known as **true characters**, and those due to homoplasy as **false characters**. The **compatibility technique** is used to find the true characters and discard the false ones. It requires that the true characters used must be compatible and consistent with one another.

**Homoplasy** between characters and character states resulting due to parallel or convergent evolution and reversals and unequal evolutionary rates along different evolutionary paths pose many problems in arriving at a parsimonious cladogram. It is very difficult to distinguish between a true and a false character. The search for true characters will involve minimizing homoplasy. The compatibility analysis tries to find a set of mutually compatible true characters (called a **clique**) and so it becomes somewhat similar to applying the rule of parsimony. Several computer programs have been written for finding the largest set of compatible characters (Estabrook, 1977).

Cladism is similar to evolutionary systematics because the comparative analysis of synapomorphies (as well as symplesiomorphies) is based on the interpretation and establishment of homologies (similarities due to common ancestry). Eldredge (1979, p. 181) stressed that synapomorphies are homologies by definition, but the converse is not true because plesiomorphies are also homologies. Patterson (1982, p. 33) explains that symplesiomorphy and synapomorphy are homologies which stand in a hierarchic relation to one another – the former is a hypothesis of a **set** (of homologies in a monophyletic group), while the latter is a hypothesis of a **subset** of that set.

Patterson (1982) stressed that synapomorphies are properties of monophyletic groups and added, ‘since synapomorphies are the **only** properties of monophyletic groups, tests of a hypothesis of homology must be other hypotheses of homology – other synapomorphies’. He summarized this problem thus, ‘If homology is the property of monophyletic groups, several consequences follow. First, homology and synapomorphy must be the same thing. Secondly, homologies must form a hierarchy. And, thirdly, non-monophyletic groups (para- and polyphyletic) cannot be characterized by homology. The only circumstance under which a paraphyletic group can be characterized by homology is if the paraphyly is caused by the removal of a monophyletic group characterized **solely** by the absence of that homology.’

Charig (1982) found a great deal of variability in the approach of cladistics from the original Hennigian pattern, and called such approaches ‘natural order systematics’, branding them as having nothing whatsoever to do with either phylogeny or evolution. He preferred to call the Simpsonian (Mayrian) and Hennigian varieties of evolutionary systematics clado-evolutionary systematics. This compromise in terminology is a step forward to uniting the two different schools of thought. After all, both try to reconstruct phylogeny on the branching pattern of evolution (although many still doubt if evolution has a branching pattern, and some even doubt the evolutionary theory itself).

Rieppel (1984, p. 31) stated, ‘Cladism is a static view of nature, a method of ordering nature according to the principle of character subordination. Evolutionism is a dynamic view of nature which adheres to the “principle of continuity”. The two methods result in complementary views of nature, just as wave and corpuscle theory are complementary views of light. The complex Whole can only be expressed by the paradox of complementarity.’

The cladistic approach was used by Baldwin and Schouest (1990), who developed a taxonomic scheme for the classification of Heteroderinae, *sensu* Luc *et al.* (1988), using computer-generated phylogenetic analyses. Newly discovered characters, such as host response, *en face* patterns, female cuticle layers and phasmid structure, were part of the matrix proposed, using in all the 19 most reliable characters

for 20 operational taxonomic units (OTUs). They used PAUP (see Fink, 1986; Platnick, 1987) as a more reliable parsimony algorithm for finding the most parsimonious phylogenetic hypothesis of the Heteroderinae.

### (v) Phenetics

This approach uses phenetic clustering methods to classify organisms on overall similarities in their structure without bothering to know how they have come about. These clustering methods are based on studying the similarity, distance and dissimilarity measures of **operational taxonomic units** (OTUs), which may be individuals, populations, species or higher categories. They help in the identification and separation of OTUs into groups and in this way can play a useful role in the morphospecies concept, but they are of little use in hierarchic classification or determining phylogenetic relationships. For Tylenchida, the phenetic approach will continue to have a major role to play since identification and, to a certain extent, classification will have to be based on the interpretation of similarities and dissimilarities of morphological data, and thus will remain to a large extent speculative.

The use of a large number of characters, as in numerical taxonomy, has yielded consistent results in developing hierarchical classification. Sokal & Sneath (1963, p. 264) stated, 'One of the attractive properties of taxonomies based on large numbers of characters is their robustness under different statistical treatments. By this we mean that a given body of data, when analyzed by different similarity coefficients or by different cluster analyses, or both, usually yields remarkably similar dendrograms and hierarchies.' They considered all characters of equal weighting and stressed 'unless and until a consistent, logically defensible system for weighting character can be provided, weighting must remain equal.' Key characters, however, are recognizable after a careful overall comparison has been made.

Moss & Webster (1970) reviewed the application of phenetics and numerical taxonomy to systematic nematology, and summed up the controversy that developed on the usefulness of this approach by saying, 'heralded as a panacea by its proponents, NT (numerical taxonomy) has been condemned as an abomination by its critics. It appears likely that both sides have an element of truth.' Numerical taxonomy has great potential in species identification and can be used in the recognition of genera and higher categories as well.

Since many Tylenchida are parthenogenetic, the concept of biological species is not applicable. Slight mutations in such forms produce biotypes which are not reproductively isolated and which are described as new species (cf. genus *Helicotylenchus*). Such phenetic species have been called thelytokous species. Multivariate analyses undertaken by Fortuner *et al.* (1984) on 28 populations of *Helicotylenchus pseudorobustus* and type populations of *H. bradys*, *H. microlobus* and *H. phalerus* confirmed that they all belong to the same species.

Blackith & Blackith (1976) used principal coordinate analysis of 34 characters in 120 individuals representing 84 nominal species of *Tylenchus*, *sensu lato*. This multivariate analysis did not produce a clear demarcation between *Tylenchus*, *Filenchus* and *Lelenchus*, but *Aglenchus* stood out as a good group, largely because of an offset head, clearly defined annules, prominent stylet knobs and median bulb and the presence of lateral vulval membranes. *Irantylenchus clavidorus* and *I. vicinus*

clustered between two groups, *Tylenchus* and *Filenchus*, while *Pleurotylenchus sachsi* and *Malenchus machadoi* fell in the *Aglenchus* group.

**Multivariate analysis programs** and **numerical taxonomic techniques** involving clustering and ordination methods to differentiate between species of *Rotylenchus* and *Orientylus* were employed by Zancada and Lima (1986). Clustering methods involved sequential, agglomerative, hierarchic and non-overlapping clustering. The average linkage clustering based on distance and correlation coefficient was used for UPGMA (unweighted pair-group method using arithmetic averages). Their numerical analysis showed a general agreement to the phenetic relationships found in *Rotylenchus* species by their authors when they proposed them.

Computer-aided phenetic identification helps in matching species data from a standardized databank in a useful comparative study which is achieved in a very short time. Statistical procedures are performed to estimate variance of species characters for identification and comparison purposes. Results are pooled to provide chi-squared values, which are low for similar and high for dissimilar species.

Interspecies morphometric comparisons using computer analysis have been made in the genera *Tylenchorhynchus* and *Merlinius* (Rey & Mahajan, 1988) and *Helicotylenchus* (Fortuner & Wong, 1984). Boag *et al.* (1989) compared three procedures – matching, modified Gower's (1971) coefficient of similarity and a statistical technique, using a desktop microcomputer, and found that the results were statistically highly correlated in ranking of species.

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# III Order Tylenchida

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## 1. ORIGIN AND PHYLOGENY

Paramonov (1962, 1967, 1968, 1970) pioneered the work on the speculative phylogeny of the Tylenchida. He believed that through a thorough study of ecological-morphological characters and ontogeny of the contemporary Tylenchida it is possible to deduce the phylogenetic relationships of various groups. Loof & De Grisse (1974), however, felt that due to the absence of fossils it was not permissible to draw phylogenetic conclusions from the morphological data alone. Unlike the barnacle, nautilus, horse and elephant, nematodes lack shells, bones or other preservable structures and can hardly be expected to provide evidence showing lineages. Nevertheless, speculative phylogenetic histories can be deduced from the data and information available from the study of modern Tylenchida. Clado-evolutionary methodologies must be employed to understand the mutual relationships of the Tylenchida groups.

### Origin of the Tylenchida

There can be no sufficient reason to doubt that the Tylenchida arose on land, but the statement that the Tylenchida originated in the Devonian Period is mere conjecture. The nematodes have a very long history of about 600 million years (cf. man's history of 1 million years or so), but as to when the tylenchid ancestor acquired a protrusible stylet is impossible to determine.

The time of the origin of the Tylenchida is thought to be about the middle of the Palaeozoic Era. Andr  ssy (1976) estimated the origin of the Tylenchida in the Cambrian or Ordovician, some 500 million years ago. Maggenti (1971) speculated that the Tylenchoidea and Aphelenchoidea evolved from a Diplogasteroidea-like ancestor, the two branches having split off during the Devonian Period, some 400 million years ago. Siddiqi (1980) also thought that the Tylenchida originated in the Devonian Period, but he emphasized the point that the Tylenchida did not share a common origin with the Aphelenchida. Whereas Tylenchida seem to have originated

from an ancestor with a non-muscular corpus bearing a feeding stylet as a boring tool, Aphelenchida's ancestor was a predator with a muscular corpus and a mechanism of injecting salivary fluid quickly into its prey. A muscular oesophageal pump developed secondarily in Tylenchida whereas it was already present in ancestral Aphelenchida.

### **Cephalobid–oxyurid origin**

Different origins of parasitism aided by the advent of a protrusible stylet in the ancestral forms must have laid the foundation for the evolution of the Hexatyulina (parasites of arthropod haemocoels) and for the Tylenchina, Hoplolaimina and Criconematina (parasites of roots) (see Fig. 13). Siddiqi (1983a) called this ancestral stock of the Tylenchida 'the Cephalobida–Oxyurida complex'. Siddiqi (1979) was the first to propose that the Tylenchida probably had a common origin with the Oxyurida. In 1980 he speculated that the Tylenchida originated from saprobiont Oxyurida-like ancestors which had a tendency towards parasitism of lower animals and plants. These animals must have been highly adaptive in nature, and possibly showing alternation of free-living and parasitic generations. Various similarities in morphological characters between the Tylenchida and Oxyurida were pointed out by him. A non-papillate male tail, a non-ribbed bursa and the genital papillae grouped around the cloacal aperture were considered by him (*loc. cit.*) as key phylogenetical characters which bring Tylenchida closer to Oxyurida than Aphelenchida, Diplogasterida and Rhabditida.

For the common ancestry of the Tylenchida and Cephalobida, Siddiqi (1980) cited the resemblances in the structure of the cuticle, lateral field, excretory system, prodelphic gonad, phasmids and the reduction of genital papillae on the male tail. He pointed out that the phasmid-like structure seen in Tylenchidae (called by him the prophasmid) was similar in structure and position to the hypodermal pores of female *Nothacrobeles* spp. which, unlike Tylenchidae, have distinct phasmids on the tail. If these two are homologous structures, then phasmids in Tylenchidae should be regarded as absent. The inverted U-shaped excretory system of Cephalobida and the asymmetrical system of Tylenchida were supposed to have been derived from a more primitive oxyuroid type.

The pattern of cuticle strata is similar in adult *Panagrolaimus* (Cephalobida) and Tylenchida in having only two strata – epicuticle and exocuticle – as compared to three strata – epicuticle, exocuticle and endocuticle – of Rhabditida, Strongylida, Ascaridida and Spirurida (Maggenti, 1979).

### **Oxyurid–drilonematid origin**

Among the likely homologies pointed out by Siddiqi (1980) between the Tylenchida and Oxyurida (including Drilonematoidea) were the following: (i) cephalic sensilla and adaptive oesophagus; (ii) aggregation of the genital papillae around the cloacal aperture; (iii) a non-papillate male tail and a non-ribbed bursa; and (iv) the excretory system. The asymmetrical excretory system of the Tylenchida can be derived from the oxyurid type through the reduction of the lateral canal of one side.

Myenchina was regarded as a suborder of Tylenchida by Siddiqi (1986) and, according to Siddiqi (1980), it was thought to share, with Drilonematoidea, a

common ancestor with the ancient Oxyurida. The non-muscular oesophagus lacking a bulb, the absence of male caudal papillae and the parasitism of the annelid coelom related Myenchina to the Drilonematina. Siddiqi (1980) pointed out that, unlike Drilonematina, Myenchina do not show drastic morphological adaptations to parasitism of the annelid coelom. Myenchina are related to Hexatylinea in the structure of the oesophagus, stylet, gonads and in coelom parasitism but are differentiated by their typical excretory system and unique muscle parasitism. However, the characteristic shape of the spicule and the excretory vesicle in Myenchina point to their separate origin from a different stock from that which gave rise to the insect haemocoelom-parasitic Hexatylinea. Myenchina is a very specialized group with a few known representatives which are poorly described. A separate order, **Myenchida**, was proposed for them by Inglis (1983). Also this group is poorly known and hence it is thought proper to exclude it from the order Tylenchida.

### Archi-Tylenchida

The relationship between fungi and nematodes must have developed quite early in their evolution. Modern Hexatylinea have members which **passively** feed on fungal hyphae. *Hexatylus* and some Anguininae have only to puncture the fungal hypha for the food to flow into the gut by the turgor pressure inside the hypha. Such forms do not have a muscular oesophageal pump; muscles developed later in the postcorporate region. They should not be confused with the Aphelenchida, whose fungal-feeding forms have a large muscular median bulb enclosing the ampulla (storage organ) of the dorsal oesophageal gland fluid for its quick injection into the fungal or animal cell. Siddiqi (1980) considered *Hexatylus* as being closest to the hypothetical ancestor of the Tylenchida.

Regarding the likely ancestor of the Tylenchida, Siddiqi (1980) wrote: 'The fore-runner of the Tylenchida was possibly a form that had a narrow tubular stoma with small needle-like metarhabdial teeth, a cylindrical, unmodified non-muscular oesophagus, oesophageal glands closely packed together around the anteriormost part of the intestine, a posterior vulva, monodelphic prodelfic gonad and an elongate tail; the male had a similar tail, simple paired spicules, an outstretched testis, genital papillae aggregated around the cloaca and lacked a bursa and gubernaculum. It was most probably a saprobiont.'

It appears very probable that the stylet appeared for plant and animal parasitism in secernentean nematodes more than once and that two major evolutionary lines – Tylenchida and Aphelenchida – are now flourishing (see Fig. 1) (Siddiqi, 1980, 1983a; Maggenti, 1982). That the Tylenchida evolved only from fungus-feeding ancestors, as was believed by Paramonov (1968, 1970), Maggenti (1971, 1978) and Andr ssy (1976), was disputed by Siddiqi (1983a) who argued, 'The different natures of the higher plant and fungus cell-wall perhaps laid the basis for two evolutionary lines: the algal cell-feeding Tylenchidae-like forms evolving to the modern Tylenchina and the fungal feeding Neotylenchoidea-like ancestors progressing towards the fungal feeding, insect-parasitic and rarely plant-parasitic Hexatylinea.'

This was the first suggestion of the evolution of the root-parasitic Tylenchina from the algal-feeding forms. It is supported by the present analysis of the Tylenchida. Root parasitism is exhibited by the Tylenchata, Hoplolaimina and Criconematina. The universal fungus feeding of the Hexatylinea is not found in



Tylenchina (except the Anguinata, which have a direct life cycle and which have evolved to become obligate parasites of plants, mostly of their above-ground parts and seeds), Hoplolaimina and Criconematina. Some Anguinoidea (*Neoditylenchus*, *Sychnotylenchus*) are found in association with xylophagous and mycetophagous insects as commensals but no instance of insect parasitism by anguinoids is known. This group (Anguinoidea) was assigned to Hexatylinea by Siddiqi (1986) and Ryss (1993), but, since it lacks insect parasitism and shares a synapomorphy of lacking phasmids and a symplesiomorphy of possessing prophasms, it is now proposed as a new infraorder Anguinata, under the suborder Tylenchina.

Chizhov & Berezina (1988) studied the female genital system of Tylenchida and proposed that Tylenchida descended from ancestral rhabditids and close groups (Rhabditida and Cephalobida). They considered *Psilenchus* as the most primitive tylenchid form, with many ancestral characters including a didelphic genital system, suggesting that the hypothetical ancestral tylenchids were didelphic. *Psilenchus* and *Antarctenchus* show many primitive characters (large postlabial amphidial apertures, weak stylet, didelphy, presence of phasmids, etc.) for the Hoplolaimina of Chizhov & Berezina (1988), but not for the Tylenchina, Criconematina or Hexatylinea, which arose from monodelphic ancestors lacking phasmids, as discussed below. There is not a single example (species) either in the Tylenchina, Criconematina or Hexatylinea which shows the primitive characters of didelphy and the presence of phasmids – the characters which otherwise should have been well distributed among the members of these groups. Hence *Psilenchus*-like forms may be regarded as ancestors of Hoplolaimina but not of either Tylenchina, Criconematina or Hexatylinea.

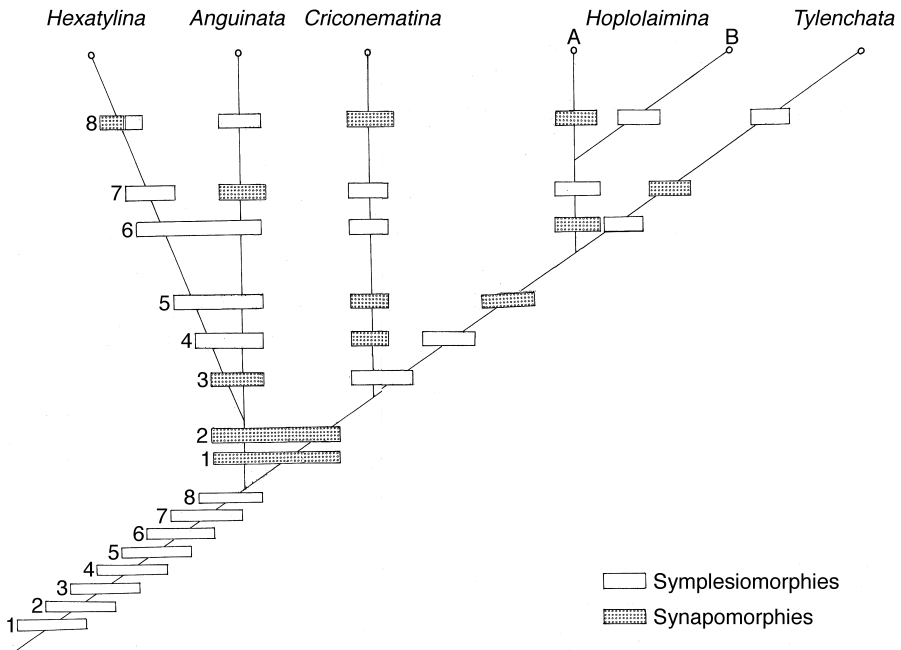
## Phylogeny of Tylenchida

Siddiqi (1986) discussed the philosophy and methodology used in the classification of Tylenchida and used a cladistic approach for higher classification. Luc *et al.* (1987) discussed the philosophy of classification of Tylenchina and, following Mayr's (1981) evolutionary school, stated, 'Mayr points out that the basic weakness of cladistics is the lack of a sensitive method of ranking, the cladist simply gives a new rank after each branching point. The evolutionary taxonomist, following Darwin, ranks data by the degree of divergence from the common ancestor, often assigning a different rank to sister groups. An example may be the family Tylenchidae and the suborder Sphaerulariina. ... Both numerical phenetics and cladistics are deemed by us to be too restrictive and limited in retrievable information to be useful in designing a higher classification.'

Construction of phylogeny, although extremely difficult for Tylenchida, is essential for building a stable hierarchic system of classification. On the tested principles outlined above in Chapter II, one should try to analyse characters, interpret homologies, examine synapomorphies and symplesiomorphies, establish monophyletic groups and speculate on the phylogenetic relationships of groups, so that a close to natural classification could be achieved.

Tylenchida *sensu* Siddiqi, 1980 appears to be a monophyletic group (see Fig. 13), members of which share several common characters and features such as:

1. A protrusible stylet.
2. A small pore-like anus in juveniles and females.



**Fig. 13.** Cladogram of the phylogeny of the Order Tylenchida based on the following synapomorphies: 1. Anus small, pore-like, directed outward. 2. Protrusible stomatal stylet present, with orifice of dorsal oesophageal gland located in the precorpus. 3. Mycetophagy, parasitism of insects and mites, and parasitism of aerial parts of plants. 4. Sperm complement produced at one stage of male development. 5. Root parasitism. 6. Didelphy and presence of phasmids. 7. Prophasmids (phasmid-like structures) present in postmedian region of body, in dorso-sublateral position near vulva. 8. Presence of sexual dimorphism in anterior region. A. Hoplolaimoidea. B. Dolichodoroidea.

3. Essentially a non-muscular oesophagus, except for the median oesophageal bulb.
4. Orifice of the dorsal oesophageal gland located in the precorpus, usually at the base of the stylet.
5. Outstretched gonoducts.
6. Oviduct with two rows of cells.
7. Paired spicules.
8. Genital papillae, if present, located around the cloacal aperture.
9. No male caudal papillae.

Lorenzen's (1981) phylogeny of the Nematoda puts tylenchs and aphelenchs together into one monophyletic group, the Tylenchida, because these groups, according to him, share synapomorphies of the presence of a stomatostylet, outstretched gonads, and both anterior and posterior branches of the female gonad lying on one side of the intestine. However, on Lorenzen's condition of holapomorphy that 'the correspondence is considered a homology', this monophyly of tylenchs and aphelenchs breaks down since, in my opinion, all these three characteristics are due to analogy and not homology, resulting from convergent or parallel

evolution. As argued by Siddiqi (1979, 1980, 1983a), tylenchs and aphelenchs did not share a common ancestor and could not be considered to constitute a monophyletic group. The nature and structure of the tylenchid stylet and oesophageal pump are quite different from those of the aphelenchs (Siddiqi, 1980).

The typical stomatal stylet and the pore-like anal characteristic of tylenchs newly discovered by Siddiqi (1980) can, however, be employed as heavyweight synapomorphies to characterize the order Tylenchida (*sensu* Siddiqi, 1986) (Figs 5 & 13). The pore-like anus directed outward seems to be a unique feature of the Tylenchida, not so far known in any other Secernentea including Aphelenchida. This is a very strong feature of Order/Class rank (cf. consistent character of the transverse slit-like anal aperture of Reptilia/Aves as compared with the circular anal aperture of Mammalia).

Maggenti (1982) classified the Tylenchida into two suborders, Tylenchina and Sphaerulariina; the latter he proposed to contain the superfamily Sphaerularioidea, which is totally entomoparasitic.

In the previous edition of this book, I had classified Tylenchida as having four suborders, Tylenchina, Hexatylinea, Criconematina and Myenchina. Recent developments in the systematics of this group include the proposal of Hoplolaimina by Chizhov & Berezina (1988), who considered three suborders, Tylenchina, Hexatylinea and Hoplolaimina, under Tylenchida. This action was based on their study of cellular structures of the female genital system and also on other morphological and ecological characters. Ryss (1993) considered Tylenchina, Hoplolaimina, Criconematina and Hexatylinea under Tylenchida, whereas Maggenti *et al.* (1987) classified Tylenchida into four suborders: Tylenchina, Aphelenchina, Sphaerulariina and Hexatylinea. Siddiqi (1989) argued in favour of accepting the suborder Hoplolaimina on the synapomorphies of paired female reproductive organs, a tricolumella and distinct phasmids. These are strong taxonomic characters in the classification of Tylenchida.

Following my previous (1986) classification and partly accepting those of Chizhov & Berezina (1988) and Ryss (1993), I consider the order Tylenchida to comprise the suborders Tylenchina, Hoplolaimina, Criconematina and Hexatylinea. However, as said above, I excluded Myenchina from the Tylenchida since Inglis (1983) considered it to represent an independent line of evolution meriting ordinal rank, Myenchida, under Tylenchia, and the information on its two families, Myenchidae (parasites of leeches in the coelomic cavity) and Myoryctesidae (parasites of amphibian muscles), is scanty and insufficient to derive proper phylogenetic conclusions. See further details of Myenchina and its relationship in Siddiqi (1986). This should help in better understanding the separate origins and evolution of Tylenchida and Aphelenchida. Now I am proposing to recognize two infraorders under Tylenchina, viz. Tylenchata and Anguinata, because they appear to have separate origins and evolutionary tendencies.

Ryss (1993) has accepted Siddiqi's (1986) concept of anguinoids belonging to Hexatylinea as primitive members on three major points: (i) mycetophagy; (ii) dorso-sublateral labial amphidial aperture; and (iii) the oesophago-intestinal valve not being tri-cellular and of oesophageal origin, but a modification of the two anterior-most cells of the intestine. Ryss (1993) pointed out that the primitive Hexatylinea were supposed to be *Ditylenchus*-like mycophagous nematodes inhabiting the litter and

the descendants of the mycophagous and phyto-mycophagous forms became entomoparasitic hexatylin with complex life cycles, including the alternation of generations or higher plant-parasitic gall-forming nematodes inhabiting the aerial parts of plants. However, anguinoids are similar to Tylenchoidea also in having phasmid-like structures (= prophasmids) (see Sturhan & Rahi, 1996). The prophasmids may be a common feature of Hexatylinea and anguinoids, but this aspect needs further research.

Siddiqi (1986) regarded Sphaerulariina, Allantonematina and Heterotylenchina as junior synonyms of Hexatylinea. Members of the type superfamilies of both Hexatylinea and Sphaerulariina show alternation of free-living fungus-feeding and entomoparasitic generations and do not show enough morphological diversity (except for the structure of the oesophagus and oviduct which are considered as characters of superfamily rank). Also, there is no taxonomic justification in regarding Sphaerulariina as different from Hexatylinea on the ground that it was proposed as one of the two suborders, while Hexatylinea was erected as one of the four suborders of the order Tylenchida. There may be some justification for recognizing Heterotylenchina (multiplication within insect host, strongly developed spicules in some genera, etc.) but until more evidence is presented, it is recognized as a superfamily, Iotonchioidea, under Hexatylinea.

## Aphelenchida a Separate Order

Siddiqi (1980) proposed, diagnosed and defined the order Aphelenchida and traced its origin and phylogeny, and compared it with the Tylenchida. On speculative matters of origin and phylogeny of the two groups, considerable difference of opinion was expressed, particularly by those who considered aphelenchs as representing a suborder of the Tylenchida. The order Aphelenchida has been recognized by Maggenti (1982), Hunt (1993) and several other nematologists. Maggenti (1982) elevated Aphelenchina to Aphelenchida and stated, 'The placement of the Tylenchida in the hierarchy of Secernentea is not a new arrangement; however, in this treatment, the aphelenchs are removed from the Tylenchida and raised to ordinal rank. Under such a system, the separate origins and evolution of the two groups can be expressed in the classification. Furthermore, the separation permits clear, unambiguous characterizations which could not be made if these groups, which represent parallel evolution, were maintained together. ... Biological evidence increasingly points to the development of the Aphelenchida separate from the Tylenchida, with both groups having their origins in the Diplogasteria. The characters that separate the two groups are clearer than is the case for most Secernentea.'

Since expressing such an unambiguous opinion about the separate origin and evolution of the Aphelenchida in 1982, Maggenti never accepted aphelenchs to represent a separate order in his later publications. In fact, in 1991 he vigorously opposed the concept of Aphelenchida having a separate origin and evolution from the Tylenchida. If one could go back in time (mentally) to the Devonian Period when stylets in Secernentea could have originated in more than one group, one might speak in terms of complexes and not orders. For example, the Oxyurida–Drilonematida complex which I used in deriving Tylenchida ancestry might have given rise to separate orders Oxyurida, Drilonematida, Myenchida, Tylenchida and the vertebrate parasites, e.g. Ascaridida and Spirurida (note that vertebrate hosts did not exist then!).

As discussed above, the Aphelenchida appear to have evolved from an ancestor with a muscular oesophageal pump which is its **primitive and universal character**. The likely common ancestor of Aphelenchida can be visualized in the Diplogasterida-like forms and not in the Oxurida–Drilonematida complex. The old concept of Paramonov (1962, 1967) that Tylenchida, including aphelenchs, evolved from a fungus-feeding form, on which later workers, including Maggenti, based their concepts, has to be rejected because such a fungus-feeding form must have lacked a muscular oesophageal pump, so characteristic of the Aphelenchida. Such a form can be visualized in the Hexatylini. Siddiqi (1980) wrote, '*Hexatylinus viviparus* is a passive feeder on fungal hyphae, force-fed by the pressure within the fungal cell on penetration by the stylet (Doncaster & Seymour, 1975). As it has no pumping oesophageal bulb and because it must maintain a low body pressure for force-feeding from the fungal cell, the rhythmic rectal pumping performs both functions, and it could be said that this species has a rectal feeding pump (Seymour, 1975). These characteristics indicate that this nematode is more of an early attempt at a plant nematode than a degenerated weed in the tylenchid garden.'

Contrary to the Aphelenchida, the Tylenchida are thought to have evolved from an ancestor with a non-muscular oesophagus lacking a feeding pump, which is its primitive and well-distributed character. Thus, both their biology and morphology point to the separate origins of these orders. The keywords for the ancestor of the two groups are: **predator** for the Aphelenchida and **borer** for the Tylenchida.

Leaving phylogenetic speculations behind, Hunt (1993) in his book on Aphelenchida stated, 'The scheme presented in this book retains the order Aphelenchida as I feel that the group is significantly distinct in both morphology and certain biological aspects to justify the rank. Morphological differences include: the position of the dorsal oesophageal gland orifice; the strongly developed, offset median bulb; the crescentic anus with overhung anterior lip in the female; the structure and development of the female and male genital tracts; ultrastructure of the large, rounded, sperm; spicule shape and in possessing caudal papillae or rays, etc.' These and other morphological characters differentiating the two orders were already discussed in detail by Siddiqi (1980).

## 1. Tylenchina

The members of the suborder Tylenchina show a great deal of numerical, morphological and evolutionary diversity. The morphological structures, especially the oesophagus, and behavioural characteristics are very variable. Two evolutionary lines – Tylenchata and Anguinata – are evident in this group. Algal and moss feeding is supposed to be the ancestral trait of the infraorder Tylenchata since several genera (*Filenchus*, *Malenchus*, *Ottolenchus*, *Tylenchus*) feed on algae, mosses and lichens and show many primitive morphological characters (weak stylet and median bulb, monodelphy, elongate tails, etc.). The evolution of the Tylenchina from algal-feeding forms was first suggested by Siddiqi (1983a) who believed that the Tylenchidae-like forms gave rise to the more advanced root-parasitic Dolichodoroidea and Hoplolaimoidea (now assigned to Hoplolaimina).

Fungal feeding is supposed to be the ancestral trait of the infraorder Anguinata. This group has a large number of fungal feeders. Plant parasitism in this group has evolved from feeding on above-ground plant parts and not on the roots. Modern

Anguinata have a large number of forms that attack seeds, inflorescence, stems and leaves. As fungal feeders, they share a common ancestor with Hexatylinea and are far removed in terms of evolutionary distance from the root-parasitic Hoplolaimina and Criconematina.

Anguinoidea and Tylenchoidea lack phasmids and share the character of monodelphy and retaining a postvulval uterine sac (cf. Hexatylinea and Criconematina which lack a postvulval uterine sac) and the presence of prophasmids and they are not root parasites of any significance. Thus they are quite different from and more primitive in terms of plant parasitism than the root-parasitic Dolichodoroidea and Hoplolaimoidea. The concepts of regarding Anguinoidea as a member of Hexatylinea and considering Hoplolaimoidea and Dolichodoroidea under a separate suborder, Hoplolaimina, do carry weight and should be given due consideration. I propose here that the infraorders Tylenchata and Anguinata be recognized under Tylenchina and Hoplolaimina accepted as a suborder (in place of the Heteroderata of Skarbilovich) for Hoplolaimoidea and Dolichodoroidea because they represent separate origins and lines of evolution.

#### (i) Tylenchata

The presence of prophasmids or phasmid-like structures being located in the submedian position (in the female near the vulva) outside the lateral field, being near and dorsal to it (Fig. 8(e)C & D), is the synapomorphy (common derived character) of Tylenchata and Anguinata. It is not yet known if Hexatylinea also share this character state. Monodelphy with a postvulval uterine sac is another synapomorphy of these groups. However, the origin and evolution of the two groups seem to be quite different and Tylenchoidea is now recognized as a monophyletic group (see Fig. 13). Siddiqi (1980) considered them as parasites of algae, mosses, pteridophytes, and of root hairs and root epidermis. The plant parasitism of Tylenchata is limited to the roots and their members are not fungal feeders or parasites of above-ground plant parts. The plant parasitism in this group shows a gradient from root surface feeders (Tylenchidae) to deep tissue feeders (Tylodoridae) but the entire group lacks features of advanced root parasitism, such as host responses, as shown by the Hoplolaimina.

#### (ii) Anguinata

As discussed above, Anguinoidea have prophasmids, lack phasmids and are monodelphic and thus are close to Tylenchoidea. However, in being fungal feeders and parasites of above-ground plant parts, they are quite apart from them. Regarding their origin, Siddiqi (1983a) wrote: 'As fungal feeders, the Anguinoidea could be quite ancient, and plant parasitism in them could have originated soon after the origin of the grasses in the Cretaceous, as indicated by their large scale parasitism of the Gramineae.'

In the previous edition of this book, Anguinoidea were classified under Hexatylinea. Due to a direct life cycle lacking an insect phase, and the presence of prophasmids, the Anguinoidea are brought back to Tylenchina but kept separate from the Tylenchoidea in a new infraorder, Anguinata.

The Anguinata are similar to most of the Hexatylinea in being fungal feeders and to *Fergusobia* in causing aerial plant galls. Although members of the Anguinata are

not known to parasitize insects or other arthropods, they are very similar in their morphology to fungus-feeding generations of *Stictylus* (now *Prothallonema*) and *Deladenus*, both having an entomoparasitic phase in their life cycle. Anguinata have no insect-parasitic phase in their life history so that it can be argued that they do not fit properly under Hexatylinea. However, some Rhabditida groups comprise forms which are free-living as well as animal-parasitic. The anguinoids may merit a separate suborder, Anguinina, as hinted by Siddiqi (1989): 'This [Hexatylinea] is an ancient group in which plant and insect parasitism might have evolved more than once. If so, then it can be argued that the suborders Hexatylinea, Sphaerulariina, Allantonematina, Heterotylenchina and Anguinina may all be valid.'

## 2. Hoplolaimina

This group is comprised of the superfamilies Dolichodoroidea and Hoplolaimoidea (including Meloidogynidae and Heteroderidae), and represents the most advanced plant root parasites. Its members lack the ability to feed on fungi. They are, unlike Tylenchata, didelphic with universal occurrence of phasmids. The group was given a subordinal rank by Chizhov & Berezina (1988). Siddiqi (1989), supporting the action of Chizhov & Berezina (1988), stated: 'This action seems justifiable because I feel that the group has its own synapomorphies in the form of paired female reproductive organs, tricolumella and a different type of spermatheca, distinct phasmids, their primary habit of root parasitism and their inability to feed on fungi, above-ground parts of plants and on insects.' Didelphy and phasmids are not seen throughout the members of Hexatylinea, Tylenchata, Anguinata and Criconematina and therefore these characters are unique for Hoplolaimina.

Ryss (1993) reviewed the structure of the lateral complex of Tylenchida and used it in deriving phylogenetic conclusions. The lateral complex includes lateral fields, amphids, deirids, phasmids and peristomal sensilla. Its analysis yielded information on the primitive taxon of the Tylenchida with a complete set of lateral complexes, as in *Psilenchus* and *Atetylenchus*, and on the evolutionary lines established by the transformation of its structures. He used Siddiqi's (1986) classification as the basis for his analysis since it 'appears to be closest to the natural order and uses the greatest number of taxonomic characters'.

### (i) Hoplolaimoidea

This superfamily is recognized by the synapomorphy of the enlargement of the sub-ventral oesophageal glands (which makes them the most advanced of root-parasitic Tylenchina) and the symplesiomorphies of the didelphy and the presence of phasmids. The families Heteroderidae and Meloidogynidae consist of members which show many advanced features (females and juveniles of third- and fourth-stage swollen, male tail reduced or absent, host specificity, etc.), on the basis of which they have been considered by several workers to constitute a separate superfamily, Heteroderoidea, and by Skarbilovich (1959) to represent a separate suborder, Heteroderata.

Siddiqi (1980) discussed in detail the likely phylogenies of Hoplolaimoidea and Heteroderoidea. The genus *Meloinema* of the Meloidogynidae has a strong stylet and cephalic framework, vermiform third- and fourth-stage juveniles, young motile females, and a rudimentary tail in the mature female – characters which link it with

members of the subfamilies Rotylenchulinae, Verutinae and Nacobbinae. This is also shown by the presence of a bursate tail in *Bursadera* which is close to *Meloinema* and *Meloidogyne*. Husain (1976), Wouts (1973) and Ryss (1980) discussed the hoplolaïmoid affinities of the Heteroderidae and Meloidogynidae. The phylogenetic schemes for these nematodes proposed by Siddiqi (1980) and Ryss (1980) support the view that Heteroderoidea and Heteroderina are synonyms of Hoplolaimoidea and Hoplolaimina, respectively.

## (ii) Dolichodoroidea

Unlike Tylenchoidea, Dolichodoroidea have distinct phasmids in the middle of the lateral fields, mostly on the tail. They have the oesophageal glands enclosed in a basal bulb and, when the glands extend over the intestine (Telotylenchinae and Belonolaiminae), it is the dorsal gland that enlarges and forms most of the glandular lobe; the subventrals do not enlarge (cf. Hoplolaimoidea). In the degree of their parasitic evolution, Dolichodoroidea occupy an intermediate position between the Tylenchoidea and Hoplolaimoidea. Ryss (1993) had concluded that Hoplolaimina consisted of two superfamilies – Hoplolaimoidea (with families Hoplolaimidae, Rotylenchulidae, Pratylenchidae, Nacobbidae, Meloidogynidae, Heteroderidae, Merliniidae, Tylenchorhynchidae and Belonolaimidae) and Dolichodoroidea (with families Dolichodoridae, Meiodoridae and Psilenchidae).

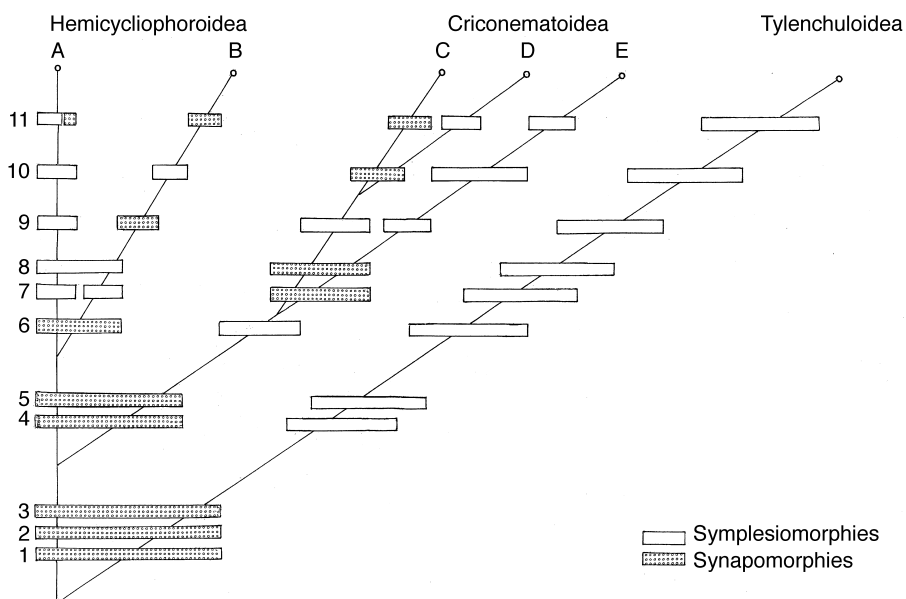
The group is comprised of two families, Psilenchidae and Dolichodoridae, of which the former appears to be more ancestral. From *Psilenchus* and *Antarctenchus* of the Psilenchidae, genera of the Dolichodoridae, such as *Macrotyphurus* and *Merlinius*, respectively, can be derived through the reduction in the tail length.

## 3. Criconematina

The entire suborder is root-parasitic and does not show mycetophagy (males and some juveniles cannot feed). Their origin is obscure, but Siddiqi (1980b) suspected it to be in the ancient Hexatyline–Myenchina complex. He pointed out that the key to the origin of the Criconematina was in the development of a large robust stylet and the correlated transformation of the broad corpus into a muscular organ (Fig. 15C). Such a transformation is seen to occur in the contemporary Hexatyline, in which the preadult heterosexual entomoparasitic female acquires a strong stylet and hypertrophied oesophagus through dimorphism. Other characters which point towards a common ancestry of the Criconematina and Hexatyline are: monodelphy with complete absence of the posterior reproductive branch, degeneration of the male stylet and oesophagus, sperm produced at one stage of the male development, single hypopytgya, and the similarities in the structure of the spicules.

On the basis of the lateral field and sense organs, Ryss (1993) assessed the relationship of Criconematina with Tylenchina and Hexatyline and remarked, 'Hexatyline differ significantly from Tylenchuloidea by the position of the amphidial aperture which is always dorso-sublateral. The presence of submerged peristomal sensilla and the criconematoid oesophagus where the procorpus has amalgamated with the metacarpus indicates that Criconematina significantly differ from Tylenchina, more so than Hexatyline differ from Tylenchina. Therefore it may be concluded that Criconematina separated before Hexatyline from the Tylenchina'.



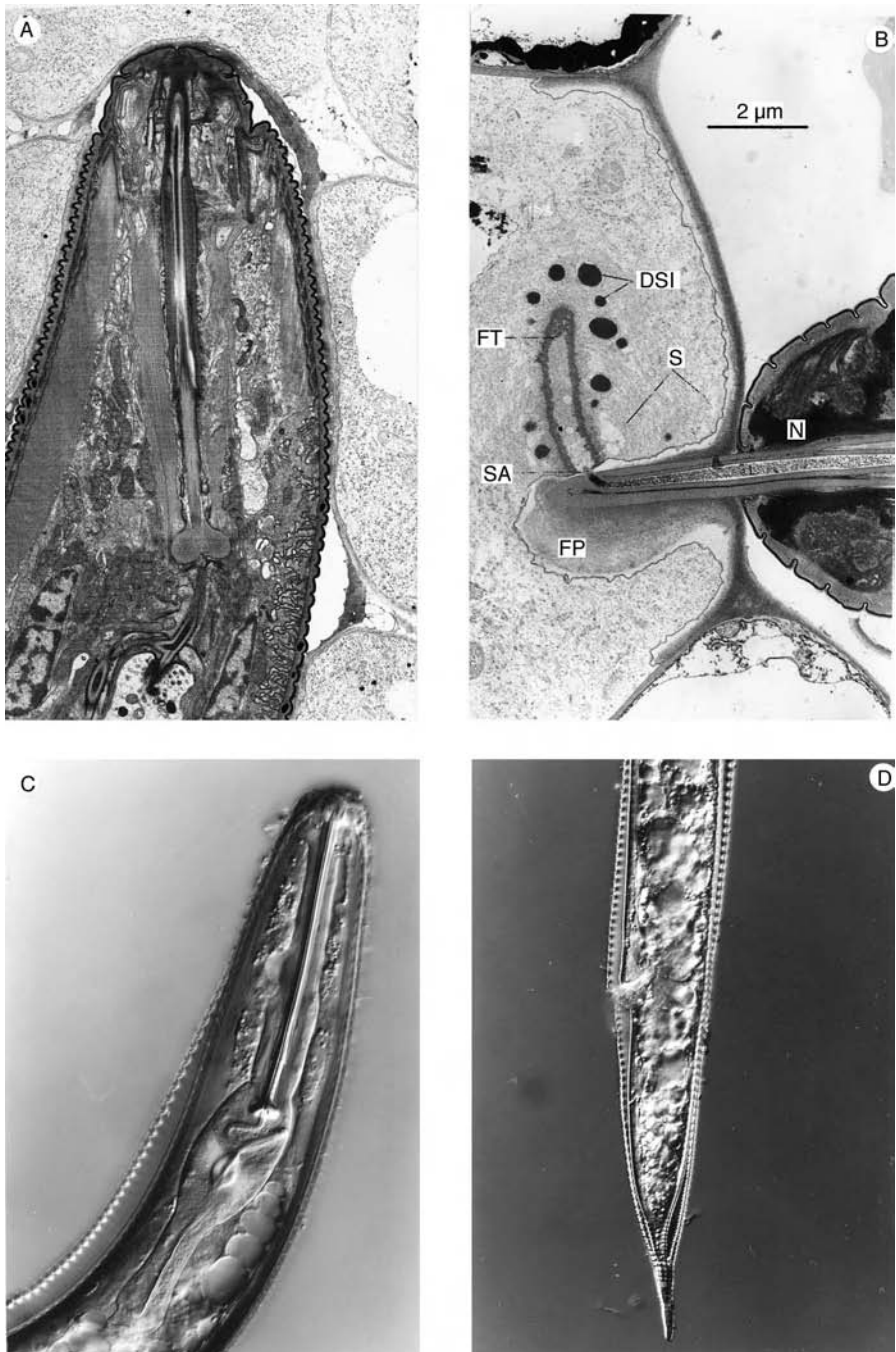


**Fig. 14.** Cladogram of the phylogeny of the Suborder Criconematina. Synapomorphies: 1. Degeneration of male stylet and oesophagus. 2. Female oesophagus with a broad muscular postcorpus (median bulb) amalgamated with precorpus. 3. Spermatheca lying ventral to gonad axis. 4. Cuticle thick, annules coarse. 5. Isthmus short and broad, amalgamated with basal oesophageal bulb. 6. Large body size. 7. Anchor-shaped basal knobs. 8. Retrorse annules. 9. Sheathed juveniles. 10. Scaled and/or spined juveniles. 11. Sheathed females. A. Caloosiidae. B. Hemicycliophoridae. C. Hemicriconemoidinae. D. Criconematinae. E. Macroposthoniinae.

The probable phylogeny of the Criconematina is shown in the cladogram (see Fig. 14). The superfamily Tylenchuloidea has members characterized by symplesiomorphies of a thin cuticle, fine round annules and the slender isthmus which is not amalgamated with the basal bulb. In contrast, Criconematoidea and Hemicycliophoroidea show the synapomorphies of the thick cuticle, coarse annules, which, in the former, are generally retrorse, and the isthmus being broad and amalgamated with the basal bulb. The Hemicycliophoroidea stand out as a unique line in the evolution of Criconematina in that the juveniles are encased in a cuticular sheath – a unique character in Tylenchida.

#### 4. Hexatylinia

There is the possibility that the parasitism of the insect haemocoel originated in different groups of nematodes, and that Sphaerulariina, Allantonematina and Heterotylenchina may prove to be valid suborders. But at present our knowledge of these nematodes is limited to findings by workers who studied the forms taken from



**Fig. 15.** A. Longitudinal section of anterior end of second-stage juvenile of *Meloidogyne incognita* inside root. (After Endo & Wergin (1973: *Protoplasma*), courtesy Springer-Verlag, Vienna.) B. Formation of feeding tube in cotton root cell by the feeding of *Rortylenchulus reniformis* (dense spherical inclusion (DSI) and swirls of endoplasmic reticulum are associated with the feeding tube (FT) formed near the stylet aperture (SA) side of the feeding plug (FP) that seals the hole made by the stylet (S) of the nematode (N). (After Rebois (1981), courtesy *Nematologica*.) C and D. Anterior and posterior regions of *Hemicycliophora* sp., respectively, from Kiel, Germany. (Courtesy U. Zunke, Germany.)

insects or mites and those who collected them from soil, fungi or plant tissues. This has meant that we do not know complete life-histories of many of these nematodes and that different genera have been proposed for different stages of the same nematode (e.g. *Prothallonema*/*Stictylus*/*Sphaerulariopsis*).

Hexatyline are highly adaptive as regards the morphology of the stylet and oesophagus and in having generation cycles in insect or mite haemocoels, in plant tissues or on fungi. It was this highly adaptive nature of these nematodes that led to the occupation of such a difficult niche as the arthropod haemocoel (see Fig. 3(a)).

The present discovery that Sphaerulariidae (e.g. *Prothallonema*) have a Paurodontidae-like free-living generation and that *Hexatyline viviparus* (Neotylenchoidea) has a dimorphic preadult female similar to that of the entomoparasitic forms raises serious questions on the relationships of the Sphaerularioidea and Neotylenchoidea. These superfamilies have mycetophagous free-living generations which are secondarily lost in some specialized parasites (e.g. *Sphaerularia*, *Iotonchium*, *Allantonema*). Although Anguinoidea have a similar morphology to that of Sphaerularioidea/Paurodontidae, they lack an entomoparasitic generation in their life cycle and are also morphologically close to Tylenchoidea. They do have a family, Sychnotylenchidae, which is closely associated with the insects and which uses them as transporters (see Fig. 3(b)). Whether sychnotylenchs have an entomoparasitic generation is not known.

*Prothallonema* and *Paurodontus* have a typical anguinoid-type oesophagus and reproductive organs. This supports Khan's (1957) finding that *Sphaerulariopsis hastatus* has oesophageal glands enclosed in a basal bulb, as found in *Stictylus*. Consequently, Khan (1960) had synonymized *Sphaerulariopsis* with *Stictylus*. This synonymy was originally proposed by Wachek (1955) but was apparently disregarded by Nickle (1963, 1967) and other workers.

Iotonchioidea of the Hexatyline have large, angular spicules not seen in any other groups of the Tylenchida. Their life cycle is similar to that of the heterotylenchs in having a parthenogenetic cycle in the insect haemocoel. The spicules in Heterotylenchinae are small and typically tylenchoid. At present, the evidence is not sufficient to justify the idea that iotonchs and heterotylenchs represent separate origins of insect parasitism and that they merit subordinal rank.

### Notes on Myenchina and Chondronematina

The Suborder Myenchina Siddiqi, 1980, comprises two genera – *Myenchus* Schuberg & Schröder, 1904 and *Myoryctes* Eberth, 1863 which, since their original description, have neither been found nor re-studied. They represent a separate origin of parasitism of the muscles and other coelomic tissues of leeches and frogs from that of the Hexatyline which parasitize insect and mite haemocoels. However, both Myenchina and Hexatyline point towards the annelid coelom parasitism of the Drilonematida with which they might be suspected of sharing a common ancestor (see Fig. 4). The systematic position of Myenchina is uncertain. It was raised to the ordinal rank by Inglis (1983). Hence Myenchina is not considered in this edition. Details of both Myenchina and Chondronematina can be found in the first edition of this book.

*Chondronema*, a genus wrongly assigned to the Allantonematidae by some workers,

is yet another example suggesting the probable origin of the Tylenchida in the ancient Oxyurida–Drilonematida complex. The genus is characterized by having a small stylet-like structure, large sucker-like phasmids and only juveniles parasitic in the insect haemocoel.

Among the stylet-bearing parasites of insects (Tylenchida, Aphelenchida and Mermithida), *Chondronema* stands out by its morphology and life-history. *Chondronema* and Mermithida are the only groups in which only juveniles are parasitic in the insect haemocoel, while the adults are free-living. Mermithida have a different oesophagus bearing stichocytes and belong to the subclass Stichosomia Siddiqi, 1983 (Siddiqi, 1983). In the first edition of this book, *Chondronema* was assigned to the Suborder Chondronematina Siddiqi, 1986, of the Order Drilonematida and is not considered further here (see details in Siddiqi, 1986).

The above discussion gives added weight to Siddiqi's (1980) supposition that 'loss of a valvate basal bulb and the papillae from the male tail and the acquisition of a primitive stylet in the ancient Thelastomatoidea of the annelids are here supposed to have given rise to coelom-inhabiting Myenchina, much in the same way as they possibly gave rise to the non-stylet bearing Drilonematoidae' (see also discussion by Poinar, 1978). This also seems to be true for *Chondronema*. It can therefore be summarized that Chondronematina, Myenchina and Hexatylinea are three separate evolutionary lines of the ancient Oxyurida–Drilonematida complex which successfully parasitized the coelom and coelomic tissues of the lower animals (see Fig. 4).

Blaxter *et al.* (1998) proposed a molecular evolutionary framework for the Phylum Nematoda on the basis of their study of the database of small subunit sequences from 53 taxa. Model phylogenies using maximum parsimony, maximum likelihood and minimum evolution utilize the neighbour-joining method. They identified three clades (supposedly monophyletic groups) within the Secernentea, one of which is 'a "cephalobid" clade, [which] groups the plant-parasitic orders Tylenchida (represented here by the cyst nematode genus *Globodera* and the root-knot nematode genus *Meloidogyne*) and Aphelenchida, the vertebrate parasitic genus *Strongyloides* and the entomopathogenic genus *Steinernema* with free-living bacteriophores of the rhabditid families Cephalobidae and Panagrolaimidae'.

Inglis (1983) proposed the Subclass Tylenchia to comprise three Orders – Tylenchida (having Suborders Tylenchina, Hexatylinea and Aphelenchina), Allantonematida and Myenchida. He also proposed the two new Orders, Allantonematida and Myenchida, the former comprising two new Suborders, Allantonematina and Heterotylenchina. I consider Tylenchida as a sole Order of the Subclass Tylenchia of the Class Secernentea. Aphelenchida, on the other hand, is considered to belong to the subclass Rhabditia.

### Systematic Position of Tylenchida Thorne, 1949

Phylum: Nematoda Rudolphi, 1808 (Lankester, 1877)

syn. Nematodea Rudolphi, 1808

Nematelmia Vogt, 1851

Nemata Cobb, 1919 (1932)

Nemathelminthes Gegenbaur, 1859

Nematelminthes Carus, 1863

Class: Secernentea von Linstow, 1905  
 syn. Phasmodia Chitwood & Chitwood, 1933  
 Secernentia Andr ssy, 1976  
 Subclass: Tylenchia Inglis, 1983  
 Order: Tylenchida Thorne, 1949  
 syn. Allantonematida Inglis, 1983

## 2. OUTLINE CLASSIFICATION OF TYLENCHIDA

In the first edition of this book, Siddiqi (1986) presented the outlines of three systems of classification of Tylenchina, viz. those of Allen & Sher (1967), Andr ssy (1976) and Siddiqi (1986). Allen & Sher (1967) used a very conservative approach since their system considered only one superfamily (Tylenchoidea) for all the tylenchs, with a minimal number of families and subfamilies. Andr ssy (1976) recognized four superfamilies (Tylenchoidea, Neotylenchoidea, Hoplolaimoidea and Criconematoidea) and a moderate number of families and subfamilies. Siddiqi (1986) divided Tylenchina into three superfamilies – Tylenchoidea (with families Tylenchidae, Ecphyadophoridae, Atylenchidae and Tylodoridae), Dolichodoroidea (with Dolichodoridae and Psilenchidae) and Hoplolaimoidea (with Hoplolaimidae, Rotylenchulidae, Pratylenchidae, Nacobidae, Meloidogynidae and Heteroderidae). Criconematids were assigned to Criconematina. In the latter half of the 20th century, most of the suborders, family ranks, new genera and new species of Tylenchida were proposed and described by the present author (see list of publications in S.F. Siddiqi & Ye, 1996).

The system of classification given by Maggenti *et al.* (1987, 1988) is supposedly based on Mayr's (1981) evolutionary concept but is a very conservative approach. Below is presented the classification of various genera of Tylenchina (including criconematids) as given by Maggenti *et al.* (1988) for comparison with the one used in this book.

### (i) Classification of Tylenchina by Maggenti *et al.* (1988)

(Synonyms of taxa are indicated by = sign)

Suborder **TYLENCHINA** Chitwood, 1950

= Heteroderina Skarbilovich, 1959

= Criconematina Siddiqi, 1980

Superfamily **Tylenchoidea**  rley, 1880

= Hoplolaimoidea Filip'ev, 1934

= Heteroderoidea Filip'ev & Schuurmans Stekhoven, 1941

= Dolichodoroidea Chitwood, 1950

= Atylenchoidea Skarbilovich, 1959

Family **TYLENCHIDAE**  rley, 1880

= Atylenchidae Skarbilovich, 1959

= Ecphyadophoridae Skarbilovich, 1959

= Boleodoridae Khan, 1964

= Tylodoridae Paramonov, 1967

Subfamily **TYLENCHINAE**  rley, 1880

= *Dactylotylenchinae* Wu, 1969

= *Duosulciinae* Siddiqi, 1979

### Genera

*Tylenchus* Bastian, 1865

= *Aerotylenchus* Fotedar & Handoo, 1979

*Miculenchus* Andr ssy, 1951

= *Ceramotylenchus* Ebsary, 1986

*Filenchus* Andr ssy, 1954

= *Ottolenchus* Husain & Khan, 1965

= *Dactylotylenchus* Wu, 1968

= *Lambertia* Brzeski, 1977

= *Duosulcius* Siddiqi, 1979

= *Zanenchus* Siddiqi, 1979

= *Discotylenchus* Siddiqi, 1980

*Malenchus* Andr ssy, 1968

= *Neomalenchus* Siddiqi, 1979

*Irantylenchus* Kheiri, 1972

*Polenchus* Andr ssy, 1980

*Allotylenchus* Andr ssy, 1984

*Cucullitylenchus* Huang & Raski, 1986

*Mukazia* Siddiqi, 1986

Subfamily ECPHYADOPHORINAE Skarbilovich, 1959

= *Epicharinematinae* Maqbool & Shahina, 1985

= *Ecphyadophoroidinae* Siddiqi, 1986

### Genera

*Ecphyadophora* de Man, 1921

= *Karachinema* Maqbool & Shahina, 1985

*Lelenchus* Andr ssy, 1954

= *Tylenchus* (*Lelenchus*) Andr ssy, 1954

*Ecphyadophoroides* Corbett, 1964

= *Tenunemellus* Siddiqi, 1986

*Epicharinema* Raski, Maggenti, Koshy & Sosamma, 1982

*Mitranema* Siddiqi, 1986

Subfamily TYLODORINAE Paramonov, 1967

= *Campbellenchinae* Wouts, 1977 [1978]

= *Eutylenchinae* Siddiqi, 1986

### Genera

*Eutylenchus* Cobb, 1913

*Macrotyrophurus* Loof, 1958

*Cephalenchus* Goodey, 1962

= *Imphalenchus* Dhanachand & Jairajpuri, 1980

*Tylodorus* Meagher, 1963

*Campbellenchus* Wouts, 1977 [1978]

Subfamily ATYLENCHINAE Skarbilovich, 1959

= *Antarctenchinae* Spaull, 1972

= *Pleurotylenchinae* Andr ssy, 1976

= *Aglenchinae* Siddiqui & Khan, 1983 [not Siddiqi & Khan]

**Genera***Atylenchus* Cobb, 1913*Aglenchus* Andrásy, 1954*Pleurotylenchus* Szczygiel, 1969*Antarctenchus* Spaull, 1972*Gracilancea* Siddiqi, 1976*Coslenchus* Siddiqi, 1978= *Cosaglenchus* Siddiqui & Khan, 1983= *Paktylenchus* Maqbool, 1983

Subfamily BOLEODORINAE Khan, 1964

= *Psilenchinae* Paramonov, 1967= *Basiriinae* Decker, 1972= *Leipotylenchinae* Sher, 1973**Genera***Psilenchus* de Man, 1921*Boleodorus* Thorne, 1941*Basiria* Siddiqi, 1959= *Clavilenchus* Jairajpuri, 1966= *Basiroides* Thorne & Malek, 1968= *Neobasiria* Javed, 1982= *Pseudobasiria* Jahan, 1986*Neopsilenchus* Thorne & Malek, 1968*Atetylenchus* Khan, 1973= *Leipotylenchus* Sher, 1974*Neothada* Khan, 1973*Duotylenchus* Saha & Khan, 1982*Basirienchus* Geraert & Raski, 1986**Genus incertae sedis***Luella* Massey, 1974**Genera dubia***Sakia* Khan, 1964*Basiliophora* Husain & Khan, 1965

Family ANGUINIDAE Nicoll, 1935 (1926)

= *Anguillulinidae* Baylis & Daubney, 1926= *Nothotylenchidae* Thorne, 1941= *Sychnotylenchidae* Paramonov, 1967= *Ditylenchidae* Golden, 1971= *Halenchidae* Jairajpuri & Siddiqi, 1969= *Pseudhalenchinae* Siddiqi, 1971= *Neoditylenchinae* Kakuliya & Devdariani, 1975= *Cynipanguininae* Fotedar & Handoo, 1978= *Nothanguininae* Fotedar & Handoo, 1978= *Thadinae* Siddiqi, 1986**Genera***Anguina* Scopoli, 1777= *Anguillulina* (*Anguina*) Scopoli, 1777= *Anguillulina* Gervais & Van Beneden, 1869 [1859]

= *Paranguina* Kir'yanova, 1955

= *Nothanguina* Whitehead, 1959

*Halenchus* Cobb, 1933

*Ditylenchus* Filip'ev, 1936

= *Anguillulina* (*Ditylenchus*) Filip'ev, 1936

= *Nothotylenchus* Thorne, 1941

= *Boleodoroides* Mathur, Khan & Prasad, 1966

= *Diptenchus* Khan, Chawla & Seshadri, 1969

= *Safianema* Siddiqi, 1980

= *Orrina* Brzeski, 1981

*Thada* Thorne, 1941

*Sychnotylenchus* Rühm, 1956

= *Neoditylenchus* Meyl, 1961

*Pseudhalenchus* Tarjan, 1958

*Subanguina* Paramonov, 1967

= *Heteroanguina* Chizhov, 1980

= *Afrina* Brzeski, 1981

= *Mesoanguina* Chizhov & Subbotin, 1985

*Cynipanguina* Maggenti, Hart & Paxman, 1974

*Pterotylenchus* Siddiqi & Lenné, 1984

**Genus incertae sedis**

*Chitinotylenchus* Micoletzky, 1922

Family DOLICHODORIDAE Chitwood, 1950

**Genera**

*Dolichodorus* Cobb, 1914

*Brachydorus* de Guiran & Germani, 1968

*Neodolichodorus* Andrassy, 1976

= *Plesiodyrus* Siddiqi, 1976

Family BELONOLAIMIDAE Whitehead, 1960

= *Telotylenchidae* Siddiqi, 1960

= *Tylenchorhynchidae* Eliava, 1974

Subfamily BELONOLAIMINAE Whitehead, 1960

**Genera**

*Belonolaimus* Steiner, 1949

= *Ibipora* Monteiro & Lordello, 1977

*Carphodorus* Colbran, 1965

*Morulaimus* Sauer, 1966

*Geocenamus* Thorne & Malek, 1968

= *Hexadorus* Ivanova & Shagalina, 1983

*Sauertylenchus* Sher, 1974

Subfamily TELOTYLENCHINAE Siddiqi, 1960

= *Tylenchorhynchinae* Eliava, 1964

= *Trophurinae* Paramonov, 1967

= *Tetylenchinae* Siddiqi, 1970

= *Merliniinae* Siddiqi, 1971

= *Meiodorinae* Siddiqi, 1976 [not 1971]



**Genera**

- Tylenchorhynchus* Cobb, 1913  
 = *Bitylenchus* Filip'ev, 1934  
 = *Telotylenchus* Siddiqi, 1960  
 = *Quinisulcius* Siddiqi, 1971  
 = *Dolichorhynchus* Mulk & Jairajpuri, 1974 nec Wiley, 1901 (Cephalochordata)  
 = *Trilineellus* Lewis & Golden, 1981  
 = *Divittus* Jairajpuri, 1984  
 = *Morasinema* Javed, 1984  
 = *Tessellus* Jairajpuri & Hunt, 1984  
 = *Neodolichorhynchus* Jairajpuri & Hunt, 1984  
*Trophurus* Loof, 1956  
 = *Clavaurotylenchus* Caveness, 1958  
*Trichotylenchus* Whitehead, 1960  
 = *Uliginotylenchus* Siddiqi, 1971  
*Nagelus* Thorne & Malek, 1968  
*Paratrophurus* Arias, 1970  
 = *Histotylenchus* Siddiqi, 1971  
 = *Telotylenchoides* Siddiqi, 1971  
*Merlinius* Siddiqi, 1970  
 = *Scutylenchus* Jairajpuri, 1971  
*Triversus* Sher, 1974  
 = *Meiodorus* Siddiqi, 1974 [1976]  
 = *Mulveyotus* Anderson & Ebsary, 1982  
*Amplimerlinius* Siddiqi, 1976

**Genus *dubium***

- Tetylenchus* Filip'ev, 1936  
 Family PRATYLENCHIDAE Thorne, 1949  
 = Nacobbidae Chitwood, 1950  
 = Radopholidae Allen & Sher, 1967  
 Subfamily PRATYLENCHINAE Thorne, 1949  
 = Radopholinae Allen & Sher, 1967  
 = Hoplotylinae Siddiqi, 1971  
 = Hirschmanniellinae Fotedar & Handoo, 1978

**Genera :**

- Pratylenchus* Filip'ev, 1936  
*Radopholus* Thorne, 1949  
 = *Radopholoides* de Guiran, 1967  
 = *Neoradopholus* Khan & Shakil, 1973  
*Pratylenchoides* Winslow, 1958  
 = *Hoplorhynchus* Andr  ssy, 1985  
*Hoplotylus* s'Jacob, 1960  
*Zygotylenchus* Siddiqi, 1963  
 = *Mesotylus* de Guiran, 1964  
*Hirschmanniella* Luc & Goodey, 1964  
 = *Hirschmannia* Luc & Goodey, 1962 nec Olofson, 1941 (Copepoda)  
*Apratylenchoides* Sher, 1973

Subfamily NACOBINAE Chitwood, 1950

**Genus**

*Nacobbus* Thorne & Allen, 1944

Family HOPLALAIMIDAE Filip'ev, 1934

= Nemonchidae Skarbilovich, 1959

= Aphasmatylenchidae Sher, 1965

= Rotylenchulidae Husain & Khan, 1965

= Pararotylenchidae Baldwin & Bell, 1981

= Interrotylenchidae Eroshenko, 1984

Subfamily HOPLALAIMINAE Filip'ev, 1934

= Rotylenchoidinae Whitehead, 1958

= Nemonchinae Skarbilovich, 1959

= Aphasmatylenchinae Sher, 1965

= Rotylenchinae Golden, 1971

= Pararotylenchinae Baldwin & Bell, 1981

= Interrotylenchinae Eroshenko, 1984

= Scutellonemoidinae Eroshenko, 1984

**Genera**

*Hoplalaimus* von Daday, 1905

= *Nemonchus* Cobb, 1913

= *Hoplalaimoides* Shakil, 1973

= *Basirolaimus* Shamsi, 1979

*Rotylenchus* Filip'ev, 1936

= *Anguillulina* (*Rotylenchus*) Filip'ev, 1936

= *Gottholdsteineria* Andr ssy, 1958

= *Orientylus* Jairajpuri & Siddiqi, 1977

= *Calvatylus* Jairajpuri & Siddiqi, 1977

= *Interrotylenchus* Eroshenko, 1984

= *Scutellonemoides* Eroshenko 1984

= *Varotylus* Siddiqi, 1986

*Helicotylenchus* Steiner, 1945

= *Rotylenchoides* Whitehead, 1958

= *Zimmermannia* Shamsi, 1973

*Scutellonema* Andr ssy, 1958

*Aorolaimus* Sher, 1963

= *Peltamigratus* Sher, 1964

= *Nectopelta* Siddiqi, 1986

*Aphasmatylenchus* Sher, 1965

*Antarctylus* Sher, 1973

*Pararotylenchus* Baldwin & Bell, 1981

Subfamily ROTYLENCHULINAE Husain & Khan, 1967

= Acontylinae Fotedar & Handoo, 1978

**Genera**

*Rotylenchulus* Linford & Oliveira, 1940

= *Spirotylenchus* (= *Spyrotylenchus*) Lordello & Cesnik, 1958

= *Leiperotylenchus* Das, 1960

*Acontylus* Meagher, 1968

*Senegalonema* Germani, Luc & Baldwin, 1984

Family HETERODERIDAE Filip'ev & Schuurmans Stekhoven, 1941

= Meloidogynidae Skarbilovich, 1959

= Meloidoderidae Golden, 1971

= Ataloderidae Wouts, 1973

Subfamily HETERODERINAE Filip'ev & Schuurmans Stekhoven, 1941

= Meloidoderinae Golden, 1971

= Ataloderinae Wouts, 1973

= Sarisoderinae Husain, 1976

= Punctoderinae Krall' & Krall', 1978

= Verutinae Esser, 1981

= Cryphoderinae Wouts, 1985

### Genera

*Heterodera* Schmidt, 1871

= *Tylenchus* (*Heterodera*) Schmidt, 1871

= *Heterodera* (*Heterodera*) Schmidt, 1871

= *Heterobolbus* Railliet, 1896

= *Bidera* Krall' & Krall', 1978

= *Ephippiodera* Shagalina & Krall', 1981

*Meloidodera* Chitwood, Hannon & Esser, 1956

*Globodera* Skarbilovich, 1959

*Cryphodera* Colbran, 1966

= *Zelandodera* Wouts, 1973

*Atalodera* Wouts & Sher, 1971

*Sarisodera* Wouts & Sher, 1971

= *Sherodera* Wouts, 1973

*Punctodera* Mulvey & Stone, 1976

*Cactodera* Krall' & Krall', 1978

*Hylonema* Luc, Taylor & Cadet, 1978

*Thecavermiculatus* Robbins, 1978

*Dolichodera* Mulvey & Ebsary, 1980

*Verutus* Esser, 1981

*Rhizonema* Cid del Prado Vera, Lownsbery & Maggenti, 1983

*Afenestrata* Baldwin & Bell, 1985

= *Afrodera* Wouts, 1985

*Bellodera* Wouts, 1985

Subfamily MELOIDOGYNINAE Skarbilovich, 1959

### Genus

*Meloidogyne* Goeldi, 1892

= *Caconema* Cobb, 1924

= *Hypsoerine* Sledge & Golden, 1964

= *Hypsoerine* (*Spartonema*) Siddiqi, 1986

### Genus *dubium*

*Meloidoderella* Khan & Husain, 1972 (in *Meloidoderellinae* Husain, 1976, *subfam. dub.*)

Subfamily NACOBODERINAE Golden & Jensen, 1974

= *Meloinematinae* (= *Meloineminae*) Husain, 1976

**Genera**

*Meloinema* Choi & Geraert, 1974

*Nacobbodera* Golden & Jensen, 1974

*Bursadera* Ivanova & Krall', 1985

Superfamily **Criconematoidea** Taylor, 1936

= Hemicycliophoroidea Skarbilovich, 1959

= Tylenchocriconematoidea Raski & Siddiqui, 1975

Family CRICONEMATIDAE Taylor, 1936

= Macroposthoniidae Skarbilovich, 1959

= Hemicycliophoridae Skarbilovich, 1959

= Madinematidae Khan, Chawla & Saha, 1975

= Caloosiidae Siddiqui, 1980

Subfamily CRICONEMATINAE Taylor, 1936

= Macroposthoniinae Skarbilovich, 1959

= Madinematinae Khan, Chawla & Saha, 1975

= Criconemellinae Khan & Saeed, 1985

**Genera**

*Criconema* Hofmänner & Menzel, 1914

= *Lobocriconema* De Grisse & Loof, 1965

= *Nothocriconema* De Grisse & Loof, 1965

= *Merocriconema* Raski & Pinochet, 1976

= *Nenocriconema* Darekar & Khan, 1981

= *Notholetus* Ebsary, 1981

= *Nothocriconemella* Ebsary, 1981

= *Paracriconema* Ebsary, 1981

= *Amphisbaenema* Orton Williams, 1982

= *Cerchnotocriconema* Bernard, 1982

*Ogma* Southern, 1914

= *Criconema* (*Variasquamata*) Mehta & Raski, 1971

= *Variasquamata* Mehta & Raski, 1971

= *Crossonema* Mehta & Raski, 1971

= *Crossonema* (*Crossonema*) Mehta & Raski, 1971

= *Crossonema* (*Seriespinula*) Mehta & Raski, 1971

= *Seriespinula* Mehta & Raski, 1971

= *Neolobocriconema* Mehta & Raski, 1971

= *Crossonema* Khan, Chawla & Saha, 1976

= *Neocrossonema* Ebsary, 1981

= *Pseudocriconema* Minagawa, 1984

= *Syro* Orton Williams, 1985

= *Ogma* (*Homogma*) Siddiqui, 1986

= *Paralobocriconema* Minagawa, 1986

= *Macrocriconema* Minagawa, 1986

*Hemicriconemoides* Chitwood & Birchfield, 1957

*Bakernema* Wu, 1964

*Criconemella* De Grisse & Loof, 1965

= *Xenocriconemella* De Grisse & Loof, 1965

= *Mesocriconema* Andrassy, 1965

= *Madinema* Khan, Chawla & Saha, 1976

= *Seshadriella* Darekar & Khan, 1981

= *Neobakernema* Ebsary, 1981

= *Crossonemoides* Eroshenko, 1981

*Discocriconemella* De Grisse & Loof, 1965

= *Neocriconema* Diab & Jenkins, 1965

= *Acrozostrom* Orton Williams, 1981

*Nothocriconemoides* Maas, Loof & De Grisse, 1971

*Blandicephalanema* Mehta & Raski, 1971

*Pateracephalanema* Mehta & Raski, 1971

= *Pateracephalanema* (*Pellipecten*) Siddiqi, 1986

### **Genera dubia**

*Macroposthonia* de Man, 1921

*Criconemoides* Taylor, 1936

Subfamily HEMICYCLIOPHORINAE Skarbilovich, 1959

### **Genera**

*Hemicycliophora* de Man, 1921

= *Procriconema* Micoletzky, 1925

= *Colbranium* Andr ssy, 1979

= *Aulosphora* Siddiqi, 1980

= *Loofia* Siddiqi, 1980

*Caloosia* Siddiqi & Goodey, 1964

= *Hemicaloosia* Ray & Das, 1978

Family TYLENCHULIDAE Skarbilovich, 1947

= Paratylenchidae Thorne, 1949

= Sphaeronematidae Raski & Sher, 1952

= Meloidoderitidae Kir'yanova & Pogosyan, 1973

= Tylenchocriconematidae Raski & Siddiqui, 1975

Subfamily TYLENCHULINAE Skarbilovich, 1947

= Sphaeronematinae Raski & Sher, 1952

### **Genera**

*Tylenchulus* Cobb, 1913

*Sphaeronema* Raski & Sher, 1952

= *Goodeyella* Siddiqi, 1986

= *Tumiota* Siddiqi, 1986

*Trophotylenchulus* Raski, 1957

= *Ivotylenchulus* Hashim, 1984

*Trophonema* Raski, 1957

*Meloidoderita* Pogosyan, 1966

Subfamily PARATYLENCHINAE Thorne, 1949

### **Genera**

*Paratylenchus* Micoletzky, 1922

= *Paratylenchoides* Raski, 1973

*Cacopaurus* Thorne, 1943

*Gracilacus* Raski, 1962

Subfamily TYLENCHOCRICONEMATINAE Raski & Siddiqui, 1975

### **Genus**

*Tylenchocriconema* Raski & Siddiqui, 1975

## II. Classification of Tylenchida (original)

Synonyms of taxa are not listed. Numbers of species described are given within parentheses: valid species in bold, synonyms in Roman and those of uncertain status in italics against the ordinal and subfamilial ranks.

### 1. *Tylenchina* Chitwood in Chitwood & Chitwood, 1950 (563, 110, 46)

#### A. *Tylenchata* Infraorder n. (373, 72, 28)

##### i. *Tylenchoidea* Örley, 1880

*Tylenchidae* Örley, 1880

*Tylenchinae* Örley, 1880 (**148**, 28, 27)

*Tylenchus* Bastian, 1865

*Aglenchus* Andrásy, 1954 (Meyl, 1961)

*Cervoannulatus* Bajaj, 1998

*Coslenchus* Siddiqi, 1978

*Cucullitylenchus* Huang & Raski, 1986

*Discotylenchus* Siddiqi, 1980

*Filenchus* Andrásy, 1954 (Meyl, 1961)

*Fraglenchus* gen. n.

*Irantylenchus* Kheiri, 1972 (Andrásy, 1976)

*Polenchus* Andrásy, 1980

*Sakia* Khan, 1964

*Boleodorinae* Khan, 1964 (**78**, 23, 0)

*Boleodorus* Thorne, 1941

*Basiria* Siddiqi, 1959

*Neopsilenchus* Thorne & Malek, 1968

*Thadinae* Siddiqi, 1986 (**8**, 0, 0)

*Thada* Thorne, 1941

*Neothada* Khan, 1973

*Duosulciinae* Siddiqi, 1979 (**80**, 11, 0)

*Duosulcius* Siddiqi, 1979

*Allotylenchus* Andrásy, 1984

*Malenchus* Andrásy, 1968

Subgenera: *Malenchus* Andrásy, 1968

*Neomalenchus* Siddiqi, 1979

*Telomalenchus* subgen. n.

*Miculenchus* Andrásy, 1959

*Mukazia* Siddiqi, 1986

*Ottolenchus* Husain & Khan, 1967 (Golden, 1971)

*Ridgellus* gen. n.

*Zanenchus* Siddiqi, 1979

*Tanzaniinae* subfam. n. (**1**, 0, 0)

*Tanzanius* Siddiqi, 1991

*Ecphyadophoridae* Skarbilovich, 1959

*Ecphyadophorinae* Skarbilovich, 1959 (**9**, 3, 0)

*Ecphyadophora* de Man, 1921

- Ultratenella* Siddiqi, 1994
- Ecphyadophoroidinae Siddiqi, 1986 (14, 1, 1)
  - Ecphyadophoroides* Corbett, 1964
  - Chilenchus* gen. n.
  - Lelenchus* Andr ssy, 1954
  - Mitranema* Siddiqi, 1986
  - Tenunemellus* Siddiqi, 1986
  - Tremonema* Siddiqi, 1994
- Atylenchidae Skarbilovich, 1959
  - Atylenchinae Skarbilovich, 1959 (1, 0, 0)
    - Atylenchus* Cobb, 1913
  - Eutylenchinae Siddiqi, 1986 (5, 1, 0)
    - Eutylenchus* Cobb, 1913
- Tylodoridae Paramonov, 1967 (Siddiqi, 1976)
  - Tylodorinae Paramonov, 1967 (3, 0, 0)
    - Tylodorus* Meagher, 1964
    - Arboritynchus* Reay, 1991
  - Pleurotylenchinae Andr ssy, 1976 (24, 5, 0)
    - Campbellenchus* Wouts, 1978
    - Cephalenchus* Goodey, 1962 (Geraert, 1968)
    - Pleurotylenchus* Szczygie , 1969
- Epicharinematinae Maqbool & Shahina, 1985 (2, 0, 0)
  - Epicharinema* Raski, Maggenti, Koshy & Sosamma, 1980
  - Gracilancea* Siddiqi, 1976

## **B. Anguinata Infraorder n. (190, 38, 18)**

### **i. Anguinoidea Nicoll, 1935 (1926)**

- Anguinidae Nicoll, 1935 (1926)
  - Anguininae Nicoll, 1935 (1926) (158, 38, 13)
    - Anguina* Scopoli, 1777
    - Diptenchus* Khan, Chawla & Seshadri, 1969
    - Ditylenchus* Filipjev, 1936
    - Indoditylenchus* Sinha, Choudhury & Baqri, 1985
    - Nothanguina* Whitehead, 1959
    - Nothotylenchus* Thorne, 1941
    - Orrina* Brzeski, 1981
    - Pseudhalenchus* Tarjan, 1958
    - Pterotylenchus* Siddiqi & Lenn , 1984
    - Safianema* Siddiqi, 1980
    - Subanguina* Paramonov, 1967
  - Halenchinae Jairajpuri & Siddiqi, 1969 (3, 0, 0)
    - Halenchus* N. A. Cobb in M. V. Cobb, 1933
  - Genus inquirendum in Anguinidae: (0, 0, 5)
    - Chitinotylenchus* Micoletzky, 1922
- Sychnotylenchidae Paramonov, 1967
  - Sychnotylenchinae Paramonov, 1967 (29, 0, 0)

*Sychnotylenchus* Rühm, 1956

*Neoditylenchus* Meyl, 1961

## 2. *Hoplolaimina* Chizhov & Berezina, 1988 (1248, 185, 56)

### i. *Hoplolaimoidea* Filipjev, 1934 (Paramonov, 1967)

*Hoplolaimidae* Filipjev, 1934 (Wieser, 1953)

*Hoplolaiminae* Filipjev, 1934 (107, 22, 6)

*Hoplolaimus* von Daday, 1905

Subgenera: *Hoplolaimus* von Daday, 1905

*Basirolaimus* Shamsi, 1979

*Ethiolaimus* subgen. n.

*Aorolaimus* Sher, 1963

*Peltamigratus* Sher, 1964

Subgenera: *Peltamigratus* Sher, 1964

*Nectopelta* Siddiqi, 1986

*Scutellonema* Andrásy, 1958

*Rotylenchoidinae* Whitehead, 1958 (295, 50, 5)

*Rotylenchoides* Whitehead, 1958

*Antarctylus* Sher, 1973

*Helicotylenchus* Steiner, 1945

*Orientylus* Jairajpuri & Siddiqi, 1977

*Rotylenchus* Filipjev, 1936

Subgenera: *Rotylenchus* Filipjev, 1936

*Calvatylus* Jairajpuri & Siddiqi, 1977, grad. n.

*Pararotylenchus* Baldwin & Bell, 1981, grad. n.

*Plesiorotylenchus* Vovlas, Castillo & Lamberti, 1993, grad. n.

*Varotylus* Siddiqi, 1986

*Aphasmatylenchinae* Sher, 1965 (4, 0, 0)

*Aphasmatylenchus* Sher, 1965

*Rotylenchulidae* Husain & Khan, 1967 (Husain, 1976)

*Rotylenchulinae* Husain & Khan, 1967 (12, 5, 0)

*Rotylenchulus* Linford & Oliveira, 1940

*Senegalonema* Germani, Luc & Baldwin, 1984

*Verutinae* Esser, 1981 (4, 0, 0)

*Verutus* Esser, 1981

*Bilobodera* Sharma & Siddiqi, 1992

*Acontylinae* Fotedar & Handoo, 1978 (1, 0, 0)

*Acontylus* Meagher, 1968

*Pratylenchidae* Thorne, 1949 (Siddiqi, 1963)

*Pratylenchinae* Thorne, 1949 (91, 20, 14)

*Pratylenchus* Filipjev, 1936

*Zygotylenchus* Siddiqi, 1963

*Hirschmanniellinae* Fotedar & Handoo, 1978 (34, 8, 1)

*Hirschmanniella* Luc & Goodey, 1964

*Radopholinae* Allen & Sher, 1967 (62, 7, 2)

*Radopholus* Thorne, 1949



- Achlysiella* Hunt, Bridge & Machon, 1989  
*Apratylenchoides* Sher, 1973  
*Hoplorylus* s'Jacob, 1960  
*Pratylenchoides* Winslow, 1958  
*Radopholoides* de Guiran, 1967  
*Zygradus* Siddiqi, 1991  
 Nacobbinae Chitwood in Chitwood & Chitwood, 1950 (2, 3, 0)  
*Nacobbus* Thorne & Allen, 1944  
 Meloidogynidae Skarbilovich, 1959 (Wouts, 1973)  
 Meloidogyninae Skarbilovich, 1959 (82, 11, 6)  
*Meloidogyne* Goeldi, 1892  
*Spartonema* Siddiqi, 1986  
 Nacobboderinae Golden & Jensen, 1974 (5, 0, 0)  
*Meloinema* Choi & Geraert, 1974  
*Bursadera* Ivanova & Krall, 1985  
 Heteroderidae Filipjev & Schuurmans Stekhoven, 1941 (Skarbilovich, 1947)  
 Heteroderinae Filipjev & Schuurmans Stekhoven, 1941 (100, 11, 3)  
*Heterodera* Schmidt, 1871  
*Afenestrata* Baldwin & Bell, 1985  
*Cactodera* Krall & Krall, 1978  
*Dolichodera* Mulvey & Ebsary, 1980  
*Globodera* Skarbilovich, 1959  
*Punctodera* Mulvey & Stone, 1976  
 Meloidoderinae Golden, 1971 (9, 0, 3)  
*Meloidodera* Chitwood, Hannon & Esser, 1956  
 Ataloderinae Wouts, 1973 (21, 0, 0)  
*Atalodera* Wouts & Sher, 1971  
*Bellodera* Wouts, 1985  
*Camelodera* Krall, Shagalina & Ivanova, 1988  
*Cryphodera* Colbran, 1966  
*Ekphymatodera* Bernard & Mundo-Ocampo, 1989  
*Hylonema* Luc, Taylor & Cadet, 1978  
*Rhizonema* Cid del Prado, Lownsbery & Maggenti, 1983  
*Sarisodera* Wouts & Sher, 1971

**ii. Dolichodoroidea Chitwood in Chitwood & Chitwood, 1950 (Siddiqi, 1986)**

- Dolichodoridae Chitwood in Chitwood & Chitwood, 1950  
 Dolichodorinae Chitwood in Chitwood & Chitwood, 1950 (26, 0, 0)  
*Dolichodorus* Cobb, 1914  
*Neodolichodorus* Andr  ssy, 1976  
 Brachydorinae subfam. n. (3, 0, 0)  
*Brachydorus* de Guiran & Germani, 1968  
 Belonolaimidae Whitehead, 1960 (Siddiqi, 1970)  
 Belonolaiminae Whitehead, 1960 (18, 1, 0)  
*Belonolaimus* Steiner, 1949

- Carphodorus* Colbran, 1965
- Ibipora* Monteiro & Lordello, 1977
- Morulaimus* Sauer, 1966
- Telotylenchidae Siddiqi, 1960
  - Telotylenchinae Siddiqi, 1960 (234, 25, 11)
    - Telotylenchus* Siddiqi, 1960
    - Bitylenchus* Filipjev, 1934 (Jairajpuri, 1982)
    - Histotylenchus* Siddiqi, 1971
    - Neodolichorhynchus* Jairajpuri & Hunt, 1984
      - Subgenera: *Neodolichorhynchus* Jairajpuri & Hunt, 1984
      - Mulkorhynchus* Jairajpuri, 1988
      - Prodolichorhynchus* Jairajpuri, 1985
  - Paratrophurus* Arias, 1970
  - Quinisulcius* Siddiqi, 1971
  - Sauertylenchus* Sher, 1974
  - Telotylenchoides* Siddiqi, 1971
  - Trichotylenchus* Whitehead, 1960
  - Trophurus* Loof, 1956
  - Tylenchorhynchus* Cobb, 1913
  - Uliginotylenchus* Siddiqi, 1971
- Meiodorinae Siddiqi, 1976 (3, 0, 0)
  - Meiodorus* Siddiqi, 1976
- Macrotriphurinae Fotedar & Handoo, 1978 (1, 0, 0)
  - Macrotriphurus* Loof, 1958
- Merliniinae Siddiqi, 1971 (111, 21, 4)
  - Merlinius* Siddiqi, 1970
  - Amplimerlinius* Siddiqi, 1976
  - Geocenamus* Thorne & Malek, 1968
  - Nagelus* Thorne & Malek, 1968
  - Scutylenchus* Jairajpuri, 1971
  - ? *Tetylenchus* Filipjev, 1936
- Psilenchidae Paramonov, 1967 (Khan, 1969)
  - Psilenchinae Paramonov, 1967 (22, 1, 1)
    - Psilenchus* de Man, 1921
    - Atetylenchus* Khan, 1973
- Antarctenchinae Spaull, 1972 (1, 0, 0)
  - Antarctenchus* Spaull, 1972

### 3. Criconematina Siddiqi, 1980 (732, 98, 28)

#### i. Criconematoidea Taylor, 1936 (1914) (Geraert, 1966)

- Criconematidae Taylor, 1936 (1914) Thorne, 1949
- Criconematinae Taylor, 1936 (1914) (210, 35, 13)
  - Criconema* Hofmänner & Menzel, 1914
    - Subgenera: *Criconema* Hofmänner & Menzel, 1914
    - Amphisbaenema* Orton Williams, 1982
    - Nothocriconemella* Ebsary, 1981

*Notholetus* Ebsary, 1981  
*Bakernema* Wu, 1964  
*Blandicephalanema* Mehta & Raski, 1971  
*Crossonema* Mehta & Raski, 1971  
*Lobocriconema* De Grisse & Loof, 1965  
*Neolobocriconema* Mehta & Raski, 1971  
*Ogma* Southern, 1914  
     Subgenera: *Ogma* Southern, 1914  
         *Croserinema* Khan, Chawla & Saha, 1976  
         *Macrocriconema* Minagawa, 1986  
         *Orphreyus* subgen. n.  
         *Pateracephalanema* Mehta & Raski, 1971  
         *Seriespinula* Mehta & Raski, 1971

Macroposthoniinae Skarbilovich, 1959 (173, 35, 10)  
*Macroposthonia* de Man, 1880  
*Criconemoides* Taylor, 1936  
     Subgenera: *Criconemoides* Taylor, 1936  
         *Criconemella* De Grisse & Loof, 1965  
         *Discocriconemella* De Grisse & Loof, 1965  
         *Nothocriconemoides* Maas, Loof & De Grisse, 1971  
         *Xenocriconemella* De Grisse & Loof, 1965

Hemicriconemoidinae Andr  ssy, 1979 (44, 8, 1)  
*Hemicriconemoides* Chitwood & Birchfield, 1957

## ii. Hemicycliophoroidea Skarbilovich, 1959 (Siddiqi, 1980)

Hemicycliophoridae Skarbilovich, 1959 (Geraert, 1966)  
 Hemicycliophorinae Skarbilovich, 1959 (138, 11, 2)  
     *Hemicycliophora* de Man, 1921  
     *Aulosphora* Siddiqi, 1980  
     *Colbranium* Andr  ssy, 1979  
     *Loofia* Siddiqi, 1980  
 Caloosiidae Siddiqi, 1980  
     Caloosiinae Siddiqi, 1980 (15, 3, 0)  
     *Caloosia* Siddiqi & Goodey, 1964  
     *Hemicaloosia* Ray & Das, 1978

## iii. Tylenchuloidea Skarbilovich, 1947 (Raski & Siddiqi, 1975)

Tylenchulidae Skarbilovich, 1947 (Kirjanova, 1955)  
 Tylenchulinae Skarbilovich, 1947 (20, 0, 0)  
     *Tylenchulus* Cobb, 1913  
     *Boomerangia* Siddiqi, 1991  
     *Trophotylenchulus* Raski, 1957  
 Sphaeronematidae Raski & Sher, 1952 (Geraert, 1966)  
     Sphaeronematinae Raski & Sher, 1952 (9, 0, 0)

- Sphaeronema* Raski & Sher, 1952
- Goodeyella* Siddiqi, 1986
- Tumiota* Siddiqi, 1986
- Meloidoderitinae Kirjanova & Poghossian, 1973 (3, 0, 0)
- Meloidoderita* Poghossian, 1966
- Paratylenchidae Thorne, 1949 (Raski, 1962)
- Paratylenchinae Thorne, 1949 (122, 6, 2)
- Paratylenchus* Micoletzky, 1922
- Subgenera: *Paratylenchus* Micoletzky, 1922
- Gracilacus* Raski, 1962
- Cacopaurus* Thorne, 1943
- Tylenchocricronematae Raski & Siddiqui, 1975 (1, 0, 0)
- Tylenchocricronema* Raski & Siddiqui, 1975

#### 4. Hexatylinea Siddiqi, 1980 (285, 20, 33)

##### i. Sphaerularioidea Lubbock, 1861 (Poinar, 1975)

- Neotylenchidae Thorne, 1941
- Neotylenchinae Thorne, 1941 (29, 4, 13)
- Hexatylus* Goodey, 1926
- Deladenus* Thorne, 1941
- Gymnotylenchinae Siddiqi, 1980 (3, 0, 0)
- Gymnotylenchus* Siddiqi, 1961
- Fergusobiinae Goodey, 1963 (7, 1, 0)
- Fergusobia* Currie, 1937 (Christie, 1941)
- Rubzovinematinae Slobodyanyuk, 1999 (1, 3, 0)
- Rubzovinema* Slobodyanyuk, 1991
- Genus inquirendum: (0, 0, 2)
- Hadrodenus* Mulvey, 1969
- Sphaerulariidae Lubbock, 1861 (Skarbilovich, 1947)
- Sphaerulariinae Lubbock, 1861 (22, 2, 3)
- Sphaerularia* Dufour, 1837
- Prothallonema* Christie, 1938
- Tripilus* Chitwood, 1935
- Paurodontidae Thorne, 1949 (Massey, 1967) (Familia dubia)
- Paurodontinae Thorne, 1949 (24, 0, 0)
- Paurodontus* Thorne, 1941
- Bealius* Massey & Hinds, 1970
- Luella* Massey, 1974
- Misticus* Massey, 1967
- Neomisticus* Siddiqi, 1986
- Paurodontella* Husain & Khan, 1968
- Paurodontoides* Jairajpuri & Siddiqi, 1969
- Allantonematidae Pereira, 1931 (Chitwood & Chitwood, 1937)
- Allantonematinae Pereira, 1931 (110, 6, 8)
- Allantonema* Leuckart, 1884

*Anandranema* Poinar, Ferro, Morales & Tesh, 1993  
*Bradynerema* zur Strassen, 1892  
*Howardula* Cobb, 1921  
*Metaparasitylenchus* Wachek, 1955  
*Neoparasitylenchus* Nickle, 1967  
*Parasitylenchoides* Wachek, 1955  
*Pratinema* Chizhov & Sturhan, 1998  
*Proparasitylenchus* Wachek, 1955  
*Protylenchus* Wachek, 1955  
*Scatonema* Bovien, 1932  
*Sulphuretylenchus* Rühm, 1956  
*Thripinema* Siddiqi, 1986  
*Contortylenchinae* Rühm, 1956 (25, 4, 0)  
*Contortylenchus* Rühm, 1956  
*Aphelenchulus* Cobb, 1921  
*Bovienema* Nickle, 1963

**ii. Iotonchioidea Goodey, 1953 (Siddiqi, 1986)**

*Iotonchiidae* Goodey, 1953 (Skarbilovich, 1959)  
*Iotonchiinae* Goodey, 1953 (15, 0, 1)  
*Iotonchium* Cobb, 1920  
*Fungiotonchium* Siddiqi, 1986  
*Paraiontonchium* Slobodyanyuk, 1975  
*Skarbilovinema* Chizhov & Zakharenkova, 1991  
*Parasitylenchidae* Siddiqi, 1986  
*Parasitylenchinae* Siddiqi, 1986 (9, 0, 0)  
*Parasitylenchus* Micoletzky, 1922  
*Kurochkinitylenchinae* Slobodyanyuk, 1999 (1, 0, 0)  
*Kurochkinitylenchus* Slobodyanyuk, 1999  
*Heterotylenchinae* Siddiqi, 1986 (8, 0, 0)  
*Heterotylenchus* Bovien, 1937  
*Paregletylenchus* Slobodyanyuk, 1984  
*Wachekitylenchus* Slobodyanyuk, 1986  
*Spilotylenchinae* Slobodyanyuk 1999 (29, 0, 0)  
*Spilotylenchus* Launay, Deunff & Bain, 1983  
*Incurvinema* Deunff, Launay & Beaucournu, 1985  
*Psyllotylenchus* Poinar & Nelson, 1973  
*Heteromorphotylenchinae* Siddiqi, 1986 (2, 0, 0)  
*Heteromorphotylenchus* Remillet & Waerebeke, 1978  
*Genera dubia in Hexatylini* (0, 0, 4)  
*Anguillonema* Fuchs, 1938  
*Helionema* Brzeski, 1962  
*Robleus* Massey, 1974

### 3. DIAGNOSIS AND RELATIONSHIP OF TYLENCHIDA

#### Order Tylenchida Thorne, 1949 syn. Allantonematida Inglis, 1983

##### Diagnosis

Subclass Tylenchia. Stylet-bearing secernentean nematodes which are free-living, mycetophagous, algal feeders or parasites of plants and arthropod haemocoels, rarely parasites of marine plants (Halenchidae); **not predatory. Alternation of free-living and insect-parasitic generations occurs in Hexatylinea.** Vermiform, not exceeding 3 mm in length (except some insect-parasitic females and uterus), some plant-parasitic (e.g. Meloidogynidae, Heteroderidae) and most insect-parasitic females become obese and partially or wholly immobile. Males and juveniles of some parasitic genera may have a degenerate oesophagus and degenerate or no stylet, and such forms do not feed. Cuticle with two main layers – epicuticle and exocuticle; endocuticle absent; with or without cuticular ridges. Cuticular outgrowths in the form of scales and spines present only in Criconematidae. It may form a hard-walled cyst in several genera of Heteroderidae. Lateral field generally with thickened cuticle present, except in females of most Criconematina with thick cuticle and coarse annules. Amphid pouch or fovea small, with pore- or slit-like aperture being lateral or dorso-sublateral (in Hexatylinea), near oral opening, or may be further behind but within the cephalic region indicated by cephalic sensilla. Deirids near excretory pore present in several groups, representing an ancestral character. Phasmids present (Hoplolaimina), punctiform, on or near tail, rarely scutellum-like and anteriorly located (Hoplolaimidae), or absent (Tylenchina, Hexatylinea, Criconematina). In Tylenchina, papilla-like **prophasmids** present in post-median position, in female near vulva. Cephalic framework six-sectored, or in some Hexatylinea eight- or 12-sectored, with light to heavy sclerotization. Oral opening a minute pore or a dorsoventral slit. Six, rarely four or eight, pseudolip areas (true lips absent, they seem to have fused, usually into a labial disc) or invaginated into oral cavity as indicated by the presence of **six inner labial** papillae or pits inside the **prestoma**. The six labial papillae around the oral aperture apparent on surface in most Hexatylinea and Tylenchina. **Cephalic papillae** four in number, may or may not be present on surface, rarely project out as cephalic setae (Atylenchidae). **The nerves of outer labial sensilla and, in most cases, the cephalic nerves, end beneath the cuticle.** Stylet composed of a conus with a subterminal ventral aperture, a cylindrical shaft (= metarhabdions) and three (one dorsal, two subventral) basal knobs (= telorhabdions), **rarely absent.** Orifice of dorsal oesophageal gland located at base of stylet or immediately behind it, always in the precorpus; those of the subventral glands near base of corpus just behind refractive thickenings of the median bulb when present. Oesophagus typically divided into a cylindrical corpus which is usually differentiated into a non-muscular **precorpus** (= procorpus), a non-muscular or muscular **postcorpus** (= metacorpus or median bulb), a slender **isthmus** crossed by a nerve ring and a basal glandular bulb or diverticulum. In insect-parasitic Hexatylinea and when degenerated (e.g. in males and juveniles of Criconematina), the entire oesophagus is non-muscular and lacks a feeding pump; a feeding function in such forms may be

performed by the rectum, e.g. *Hexatylos*. Oesophago-intestinal valve present, a cellular cardia present or absent. Excretory system of asymmetrical type with a single lateral renette cell at the end of the posteriorly directed lateral canal which is an extension of the medio-ventral terminal canal. Excretory pore mostly in nerve ring region but may be shifted as a parasitic adaptation far anteriorly (e.g. *Meloidogyne*, *Misticus*) or posteriorly (e.g. *Tylenchulus*); the renette cell may produce the gelatinous matrix in which eggs are deposited (e.g. *Tylenchulus*). Female reproductive system monodelphic-prodelphic in Hexatylini and Criconematina (which generally lack a postvulval uterine sac) and Tylenchina (which generally have a postvulval uterine sac); didelphic in Hoplolaimina, in which pseudo-monoprodelphy may occur by the loss of the posterior branch. **Ovaries telogonic** (cells dividing in the apical zone and not along the entire length of the ovary), **outstretched**, becoming reflexed or coiled secondarily due to lack of space for growth. Oviparous or ovoviviparous. Eggs oval, with smooth surface; first moult invariably occurring within the egg (two moults may occur inside egg as in *Sphaeronema*). **Oviduct with two rows of cells**. Uterus usually with a muscular and a glandular part (= **crustaformeria** or **columnella**), distal portion of which usually forms a spermatheca, specialized muscular ojector absent. Uterus may occasionally be everted (e.g. *Sphaerularia* has a fully everted uterus leading a life independent of the mother and which has been named the **uterium** by Siddiqi, 1986) or transformed into a protective cyst (e.g. *Meloidoderita*). Vagina short, not tuboid, mostly comprised of vagina vera, shorter than a body width, rarely sclerotized. Vulva a transverse slit (rarely pore-like), may have cuticular lateral flaps and anterior and/or posterior epitygma. Male reproductive system monorchic (two testes may occur due to sex reversal in some *Meloidogyne* spp.) with anteriorly outstretched testis (may be reflexed secondarily). Sperm round, amoeboid, rod-like or vermiform as in species of *Radopholus*, usually small sized and with **nucleus not showing discrete chromosomes**. **Spicules paired**, rarely of different sizes and shapes, cephalated, ventrally arcuate, **not rose-thorn shaped**. Gubernaculum fixed or protrusible, may have titillae and telamon (e.g. Hoplolaimidae), rarely absent (e.g. *Gymnotylenchus*). **Bursa** or caudal alae usually present, simple or lobed but **never with papillary ribs** although a pair of pseudoribs formed by the extension of phasmids may be present, never present only at the tail tip. **Caudal papillae absent; genital papillae one to four grouped around cloacal aperture**, mostly on its ventral side (called hypopygma, plural hypopygmata), or one or two located midventrally behind the cloacal aperture (*Fungiotonchium*). Intestine usually syncytial lacking a distinct lumen. Rectum distinct, or indistinct, in Hexatylini may act as a feeding pump. **Anus inconspicuous, minute pore-like, directed outward**. Development through four stages of juveniles which have a stylet except in some genera of Criconematina and occasionally in some genera of Hoplolaimina and Hexatylini. **Algal and fungal feeders and parasites of plants and of insect and mite haemocoels**.

Type genus

*Tylenchus* Bastian, 1865

Type suborder

Tylenchina Chitwood in Chitwood & Chitwood, 1950

### Other suborders

- Criconematina Siddiqi, 1980
- Hexatylinea Siddiqi, 1980
- Hoplolaimina Chizhov & Berezina, 1988

### Relationship

Among the various orders of the Secernentea, the order Tylenchida has convergent evolutionary similarities with the order Aphelenchida Siddiqi, 1980 due to the development of a protrusible stylet and its associated muscles and resulting modifications in the structure of the cephalic region, stoma and oesophagus and the parasitism of plants and insects. The major differences between the two orders are given below.

#### **Tylenchida**

1. Amphids mostly lateral in position.
2. Stylet shaft mostly formed by metarhabdions, lacking innervation; basal knobs formed by telorhabdions, often well developed and marked off.
3. Orifice of dorsal oesophageal gland in precorpus at the base of the stylet or a short distance behind it.
4. Median oesophageal bulb, if present, without a muscular valve anterior to the central valve-like cuticular thickening.
5. Anus inconspicuous, minute, pore-like, directed outward.
6. Sperm usually small-sized, nucleus not showing discrete chromosomes.
7. Male caudal papillae absent; bursa lacking papillary ribs or rays, never present only at the tail tip.
8. Spicules not thorn-shaped.

#### **Aphelenchida**

1. Amphids latero-subdorsal in position.
2. Stylet shaft mostly formed by telorhabdions, anteriorly innervated; basal knobs not a separate entity but represented by thickenings, not marked off from each other at the basal region of the shaft.
3. Orifice of dorsal oesophageal gland in muscular postcorpus anterior to the central valve-like cuticular thickening.
4. Median oesophageal bulb always present, with a muscular valve anterior to the central valve-like cuticular thickening.
5. Anus conspicuous (except when in a degenerate state), large, crescentic, backwardly directed slit.
6. Sperm large-sized, nucleus showing discrete chromosomes.
7. Male caudal papillae present; bursa with papillary ribs or rays when it is large and envelops the entire tail; a short bursa only at the tail tip present in several genera.
8. Spicules mostly thorn-shaped.



The Order Tylenchida was proposed by Thorne (1949) and is the sole member of the Subclass Tylenchia Inglis, 1983. Tylenchia is differentiated among the Class Secernentea by the small, minute pore-like anus, and, except for Aphelenchida, in having a protrusible stylet. The Order Aphelenchida is close to the Diplogasterida (see Siddiqi, 1980) and both belong to the Subclass Rhabditia.

#### 4. KEY TO SUBORDERS OF TYLENCHIDA

1. Arthropod-parasitic cycle involving adult female in insect or mite haemocoel present; free-living mycetophagous or non-root phytoparasitic generation cycles may or may not be present; median oesophageal bulb absent ..... **Hexatylinea**  
 Arthropod-parasitic cycle absent; single generation cycle with only fungal or phytoparasitic forms present; median oesophageal bulb usually present ..... 2
2. Monodelphic with no postvulval uterine sac; phasmid or prophasid absent; spermatheca ventral to gonad axis; hypopygma single; male oesophagus degenerate ..... **Criconematina**  
 Didelphic, if monodelphic then usually with a postvulval uterine sac; phasmid or prophasid present; spermatheca not ventral to gonad axis; hypopygma double; male oesophagus rarely degenerate ..... 3
3. Didelphic; phasmids present ..... **Hoplolaimina**  
 Monodelphic; phasmids absent ..... **Tylenchina**

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# IV Suborder Tylenchina

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## SUBORDER TYLENCHINA CHITWOOD IN CHITWOOD AND CHITWOOD, 1950

### Diagnosis

Tylenchida. Algal and moss feeders, fungal feeders (Anguinata) and parasites of lower and higher plants, attacking subterranean parts, **not parasitic in animals**. **Males with normal oesophagus and stylet. Sexual dimorphism in anterior region absent. Cuticle without distinct outer and inner layers**, variable in degree of thickness and size of annules. **Phasmids absent. Prophasmids** (papilla-like sensilla near vulva or at about the same position on male body) **located just dorsal to lateral field present**. Cuticle smooth or distinctly annulated, sometimes marked with longitudinal striae or grooves, **but annules never retrorse or with scales, spines, appendages or a double cuticle**. Cephalic region smooth or annulated; framework with light, rarely heavy sclerotization. Labial plate with six inner labial sensilla in the form of papillae or pits around a pore-like round or oval oral opening; prominent labial disc rarely present, **six outer labial sensilla not on surface**; four cephalic sensilla on surface usually present; amphidial apertures labial, sometimes just postlabial. Stylet generally small (10–15  $\mu\text{m}$ ); conus normally less than half its total length, elongate in forms with very long stylet; knobs small and rounded, never large and anchor-shaped as in Criconematoidea of Criconematina. Precorpus (= procorpus) cylindroid or fusiform; postcorpus or median bulb usually muscular with refractive thickenings but not amalgamated with precorpus into a large muscular cylinder. **Isthmus elongate, slender**. Oesophageal glands forming a basal bulb or rarely extending over intestine. **Oesophago-intestinal valve** (= cardia) **three-celled**, reduced in forms with overlapping glands or absent, as in Anguinata, represented by two anteriormost cells of the intestine. **Nerve ring circum-oesophageal**. Excretory pore in oesophageal region, renette cell post-oesophageal; excretory duct not vesiculate distally. Intestine usually syncytial, usually not extending into tail cavity. Rectum

and anus normally distinct; latter pore-like, outwardly directed. **Tails similar between sexes**, elongate-tapering, filiform, or short and different between sexes (Synchotylenchidae). **Female reproductive system monodelphic, prodelphic**, usually with a postvulval uterine sac. Vulva postmedian or more posterior. **Crustaformeria normally with less than 20 cells arranged in** a quadricolumella (Anguinoidea) or tricolumella (some Tylenchoidea). Spermatheca round, elongate, lobed, axial or offset, never ventral to gonadal axis. Ovary normally outstretched and with serially arranged oocytes, rachis present in some obese Anguinoidea. **Oesophagus and stylet normally developed in male**. Testis single, outstretched; **spermatogenesis continues in adult life**. Spicules paired, cephalated, arcuate, distally round to pointed with sensory pore ventrally subterminal; never setaceous or U-shaped. Gubernaculum generally simple, fixed. Bursa **simple or lobed** (absent in *Atylenchus*, *Miculenchus*, *Tanzanius*), not enveloping entire tail (except in *Neoditylenchus*, *Synchotylenchus*), **without phasmidial pseudoribs**. Cloacal lips seldom forming a penial tube (tubus); **hypopygium on posterior lip, if present, double**. **Juveniles**: Similar to female in most details. Algal, fungal or plant root feeders, or parasites of above-ground plant parts.

Type genus

*Tylenchus* Bastian, 1865

Type infraorder

Tylenchata infraord. n.

Other infraorder

Anguinata infraord. n.

### Key to infraorders of Tylenchina

1. Amphidial apertures minute oblique slits on raised areas on labial plate; cardia absent; fungal feeders and/or parasites of above-ground plant parts ... **Anguinata**  
 Amphidial apertures not minute oblique slits on raised areas on labial plate but variously modified from pore to large sinuate slits; cardia present; algal and root feeders, not fungal feeders or parasites of above-ground plant parts ... **Tylenchata**

Relationship and remarks

Tylenchina differs from Hexatylinea in lacking insect parasitism, nerve ring always circum-oesophageal, and presence of prophasms. Fortuner & Raski (1987), in their review of Neotylenchoidea, accepted Hexatylinea with only one genus *Hexatylys*. The closely related genus *Deladenus* was removed from *Hexatylys* and assigned to the insect-parasitic Allantonematoidea. Siddiqi (1986) had pointed out that insect-attacking female stages of *Hexatylys viviparus* were known and the genus should be classified with *Deladenus* in Hexatylinea. Tylenchina differs from Hoplolaimina in having prophasms, lacking phasms and in being monodelphic.

Tylenchina can be differentiated from Criconematina by the structure of the oesophagus in females and juveniles, well-developed male oesophagus, different face-view structures, especially due to the absence of lateral oral liplets and

submedian lobes, spermathecae well formed and not ventrally or subventrally located, a continuous spermatogenesis in the male, differently shaped spicules, paired hypopygium on the posterior cloacal lip, and the absence of retrorse annules, cuticular scales, spines or other configurations and of a body sheath and anchor-shaped stylet knobs.

Chitwood in Chitwood & Chitwood (1950) proposed the subordinal name Tylenchina without a diagnosis or an indication that it was a new taxon. Almost simultaneously, Thorne (1949) proposed and diagnosed the order Tylenchida. The ordinal names should be considered as of coordinate status as are the familial, generic and species group names, and hence Thorne (1949) should have been the authority for the subordinal name Tylenchina as well. However, the International Commission on Zoological Nomenclature was unable to propose rules for this or higher categories since its mandate does not cover taxa above the rank of superfamily. I, therefore, affirm my earlier policy (Siddiqi, 1980, p. 144, footnote) to consider that the authorities for ordinal and higher ranks are those that have actually used the particular taxonomic name for the first time, and that the endings of the names are after the Pearse (1936) system.

Sphaerulariina, proposed by Maggenti (1982) as a sister suborder of Tylenchina under the order Tylenchida, is regarded here as a junior synonym of Hexatylinea Siddiqi, 1980, due to the juniority in publication and because their type genera belong to the same group. Heteroderata was used by Skarbilovich (1959) as one of the two subdivisions of the Tylenchida. The concept of Heteroderata is different from the Hoplolaimina of Chizhov & Berezina (1988), which is based on a senior family group name. Hoplolaimina is recognized here as a suborder of Tylenchida.

## INFRAORDER TYLENCHATA INFRAORD. N.

### Diagnosis

Suborder Tylenchina. Usually small nematodes under 1 mm long, but may reach a length of 2 mm. Lateral field (a stretchable zone of cuticle) with one to six incisures, rarely obscure (e.g. *Ecphyadophora*, *Polenchus*, *Cervoannulatus*). Cephalic region variable from low flat to high, continuous to offset; framework poorly developed, usually with high arches, **rarely sclerotized**. Labial plate with six labial sensilla in the form of papillae or pits around a pore-like round or oval oral opening; prominent labial disc rarely present, and four submedian **cephalic sensilla usually on surface**. Amphidial apertures pore- or slit-like, **usually extending along the lateral sides of cephalic region**. Deirids almost always present, near level of excretory pore. **Phasmids absent. Prophasmids present**. Stylet generally small (10–15  $\mu\text{m}$ ) and weak (Tylenchidae) with a conus less than half total stylet length, or strong and elongate (Tylodoridae); basal knobs generally small, rounded, occasionally absent (e.g. *Neopsilenchus*, Thadinae; subventrals absent in *Irantylenchus*) or enlarged (*Tanzanius*), but never with outer margins directed anteriorly or anchor-shaped; protractor muscles divergent or tubular. Orifice of dorsal oesophageal gland generally 1–4  $\mu\text{m}$  (but in Boleodoridae at a greater distance) behind stylet base. Corpus elongate, slender (except *Tanzanius*); precorpus (procorpus) elongate-cylindroid, lacking musculature. Postcorpus (= metacorpus) or median bulb present or absent, muscu-

lar, or non-muscular, with or without inner refractive thickenings (valvate or non-valvate), **smaller than basal bulb, and not occupying entire body width cavity**. Isthmus elongate-slender. Basal or terminal oesophageal bulb enclosing oesophageal glands present; occasionally (e.g. *Ecphyadophora*, *Epicharinema*) only the dorsal gland may form a short lobe over the intestine. Cardia (oesophago-intestinal valve) present, prominent, tri-cellular. Intestine often with refractive granules, lumen obscure except near oesophagus and rectum. Rectum and anus distinct. **Tails similar between sexes, elongate-tapering, usually filiform. Bursa adanal** (absent in *Atylenchus*, *Miculenchus*, *Tanzanius*), **simple or lobed, not supported by phasmidial pseudoribs**. Vulva a transverse slit, lips usually not modified, usually postmedian, never subterminal or terminal; epiptygma usually absent. Glandular part of uterus tri- or quadricolumellate. Spermatheca thin-walled, round, oval or elongate sac-like, offset or axial. Ovary single, anteriorly outstretched (except with single or double flexures in *Campbellenchus*), with oocytes mostly in a row. **Postvulval uterine sac shorter than body width** or in some genera absent. Testis single, anteriorly outstretched, with tip rarely reflexed; sperm small to moderately large, round, with little cytoplasm. Spicules paired, similar, cephalated, ventrally arcuate, rarely straight (*Ecphyadophora*), neither abnormally thickened and reinforced nor setose; distal end narrow, with subterminal aperture ventrally placed. **Gubernaculum simple trough-shaped, fixed, not protrusible**, without titillae or telamon (= capitulum). Algal and root feeders, not parasites of above-ground plant parts.

#### Type genus

*Tylenchus* Bastian, 1865

#### Type superfamily

Tylenchoidea Örley, 1880 (Chitwood & Chitwood, 1937)

No other superfamily.

#### Relationship

In being monodelphic and lacking phasmids, Tylenchata differs from Anguinata in having variable shape of cephalic region and amphidial apertures, cuticle variable in thickness and annulation, a distinct cardia, usually small offset spermatheca, small-sized sperm and in lacking mycetophagy and parasitism of above-ground plant parts.

### **SUPERFAMILY TYLENCHOIDEA ÖRLEY, 1880 (CHITWOOD & CHITWOOD, 1937)**

**syn. Atylenchoidea Skarbilovich, 1959 (Golden, 1971)**

#### Diagnosis

With the characters of the infraorder Tylenchata.

#### Type family

Tylenchidae Örley, 1880

### Other families

Atylenchidae Skarbilovich, 1959

Ecphyadophoridae Skarbilovich, 1959

Tylodoridae Paramonov, 1967

### Key to families of Tylenchoidea

1. Cephalic setae present ..... **Atylenchidae**  
    Cephalic setae absent ..... 2
2. Stylet over 24  $\mu\text{m}$  long, if shorter then about as long as precorpus, with  
    tubular protractors ..... **Tylodoridae**  
    Stylet under 24  $\mu\text{m}$  (generally 8–16  $\mu\text{m}$ ) long, not as long as precorpus,  
    generally with divergent protractors ..... 3
3. Body extremely attenuated ( $a = 50\text{--}150$ ), appearing glass fibre-like; bursa  
    often lobed ..... **Ecphyadophoridae**  
    Body not extremely attenuated, not appearing glass fibre-like; bursa not  
    lobed ..... **Tylenchidae**

## FAMILY TYLENCHIDAE

### (Algal, lichen, moss feeders and root surface feeders)

Members of this family are cosmopolitan. They are encountered in large numbers in extractions from soils rich in algae and mosses. On the evolutionary ladder of modern Tylenchida, they represent the first rung in being both weak plant parasites and as a conservative group with many ancestral characters (e.g. weak feeding apparatus, undifferentiated non-muscular corpus, filiform tails, etc.).

Andrássy (1979) collected representatives of the Tylenchidae from 86 countries, states and islands and Bütschli (1873) found *Tylenchus davainei* and *Tylenchus filiformis* (now the type species of *Filenchus*) in soil under moss. Siddiqi & Hawksworth (1982) reported the finding of *Ottolenchus cabi* in association with a lichen, *Cladonia glauca*, and speculated that it was feeding on the algal part of the lichen. Siddiqi (1983a) regarded Tylenchidae as weak parasites of plants, several genera (*Tylenchus*, *Filenchus*, *Ottolenchus*) feeding on soil and freshwater algae and parasitizing lichens and mosses. They do not cause economic losses to crops.

The genus *Tylenchus* was proposed by Bastian (1865) and the family Tylenchidae was established by Örley (1880). Baylis & Daubney (1926) synonymized *Tylenchus* with *Anguillulina*, proposed by Gervais & Van Beneden (1859) for the wheat-gall nematode, later synonymized with *Anguina* by Chitwood (1935); and Goodey (1932) transferred a large number of species from *Tylenchus* to *Anguillulina*. Filipjev (1934) recognized *Tylenchus* with two subgenera – *Tylenchus* for *T. davainei* and *Anguillulina* for *T. tritici* (the wheat-gall nematode). In Tylenchinae, Filipjev assigned *Ecphyadophora*, *Eutylenchus*, *Neotylenchus*, *Psilenchus* and a number of diverse genera, e.g. *Aphelenchoides*, *Aphelenchus*, *Heterodera*, *Pratylenchus* and *Tylenchorhynchus*.

Micoletzky (1922) proposed the subgenus *Chitinotylenchus* and assigned it to *Tylenchus*. *Bitylenchus* as a subgenus of *Tylenchus* was proposed by Filipjev (1934a). *Bitylenchus* is here recognized as a genus and assigned to Telotylenchinae. Three sub-

genera of *Tylenchus* (*Aglenchus*, *Filenchus* and *Lelenchus*) were proposed by Andr ssy (1954) and raised to genera by Meyl (1961). The genus *Lelenchus* was synonymized with *Filenchus* by Andr ssy (1976). Siddiqi & Hawksworth (1982) examined the lectotype, designated by Loof (1961), of *Tylenchus leptosoma* de Man, 1880, obtained from Amsterdam Museum, and found it to be flattened so that characters such as incisures in the lateral fields, important in deciding its identity and systematic position, could not be studied. Siddiqi (1986) regarded *Lelenchus* as *genus dubium*. Raski & Geraert (1986) re-diagnosed the genus in their study of the type species from several localities. They assigned it to the subfamily Ecphyadophorinae. This action is followed here.

In 1962, Goodey proposed the subgenus *Cephalenchus* under *Tylenchus* with *T. (Cephalenchus) megacephalus* as the type species. Geraert (1962) published the description of *Tylenchus hexalineatus* and in 1964, Geraert & Goodey synonymized *T. (C.) megacephalus* with *T. (C.) hexalineatus*. In the same year Colbran synonymized the two species with *T. (C.) emarginatus*. Siddiqi (1963b) and Egunjobi (1967) proposed *T. (C.) leptus* and *T. (Aglenchus) whitus*, the latter species becoming a junior synonym of *T. emarginatus*. *Cephalenchus* was raised to genus by Golden (1971) and Siddiqi (1971) and now is recognized as a member of the Tyldoridae.

The subgenus *Ottolenchus* of *Tylenchus* was erected by Husain & Khan (1967) and was raised by Wu (1970). Golden (1971) synonymized the subgenus *Ottolenchus* with the subgenus *Aglenchus*. Siddiqi (1979) classified *Ottolenchus*, due to its lateral field comprising one ridge (two incisures), with *Miculenchus*, *Malenchus* and his new genera *Duosulcius*, *Neomalenchus* and *Zanenchus* as members of a new subfamily, Duosulciinae. Bello (1971) and Raski & Geraert (1987) regarded *Ottolenchus* as a synonym of *Filenchus*. Brzeski (1982) reviewed the taxonomy of *Ottolenchus*, considering it a valid genus. Siddiqi & Lal (1992) re-emphasized the characters differentiating *Ottolenchus* from *Filenchus* (lateral field, cephalic region, amphidial aperture shape, etc.), described 15 new species of the genus and transferred *Filenchus norman-jonesi* Raski & Geraert, 1987 and *F. resisus* Grewal, 1991 to *Ottolenchus*. *Filenchus* and *Ottolenchus* are re-diagnosed here to evaluate their relationship.

Raski & Geraert (1987) reviewed the genus *Filenchus* and proposed *Ottolenchus* Husain & Khan, 1965, *Duosulcius* Siddiqi, 1979, *Zanenchus* Siddiqi, 1979 and *Discotylenchus* Siddiqi, 1980 as synonyms of *Filenchus*. They differentiated *Filenchus* from *Tylenchus* by the conus being less than 0.3–0.4 of stylet length vs. 0.5 in *Tylenchus*, and elongate slit-like amphidial apertures extending three to four annules from the labial plate vs. large, pit-like, essentially confined to the labial plate in *Tylenchus*. In *Duosulcius* and *Zanenchus*, the amphidial apertures are pore-like and located within the labial plate and not elongate slits extending along the lateral sides of the cephalic region (see also Talavera & Siddiqi, 1996). Also, these genera have a different cuticle with deep striations and ornamented, often zig-zag, annules and narrow lateral field with single, elevated ridge, from *Filenchus* and hence should not have been synonymized with that genus. The broad, catch-all definition of *Filenchus* given by Raski & Geraert (1987) is, therefore, rejected and I agree with Andr ssy's (1988) opinion: 'The author calls the attention that it is not lucky to gather very different species in a sole genus (see *Filenchus* in sense of Raski and Geraert, 1987), since if we want to outline it, we cannot give an unambiguous definition and have too often to say "either – or".'

*Discotylenchus* has a cephalic disc and longitudinal amphidial slits, which in *D. discolabialis* are slightly sinuate, extending down to base of stylet or 6  $\mu\text{m}$  from the anterior end. The cephalic disc and amphidial apertures are similar to those in *Cucullitylenchus* Huang & Raski, 1986.

*Basiria* was proposed by Siddiqi (1959), synonymized with *Filenchus* by Goodey (1963), rediagnosed and reinstated by Siddiqi (1963a), resynonymized to *Filenchus* by Jairajpuri (1966) and revalidated by Geraert (1968) and Thorne & Malek (1968). The related genera *Neopsilenchus*, *Basiroides* and *Clavilenchus* went through a similar process of synonymization and desynonymization with the result that *Basiroides* and *Clavilenchus* are now accepted as synonyms of *Basiria*. *Basiriinae* was proposed by Decker (1972), recognized by Andr  ssy (1976), but was synonymized with *Boleodorinae* by Brzeski & Sauer (1983).

The discovery of prophasmids (phasmid-like structures) in a postmedian position on the body, just outside the lateral fields, in members of the Tylenchidae by Siddiqi (1978) paved the way for recognizing the Tylenchoidea as separate from the Dolichodoroidea and Hoplolaimoidea (which have phasmids in the middle of the lateral fields, mostly in the tail region) (Fig. 8(e) C and D; Fig. 13). Prophasmids have also been detected in the Anguinidae (Sturhan & Rahi, 1996) and represent a symplesiomorphic character of the two groups. Unlike Anguinoidea, Tylenchoidea have a different face view, a cellular cardia of oesophageal origin and are not mycetophagous or parasites of above-ground plant parts.

This shows that, due to their great diversity in number and kind, members of the Tylenchata have great taxonomic attraction, which provides for a large field of action both for the enthusiastic splitters and the not-so-enthusiastic lumpers. A typical example of the state of Tylenchida taxonomy is the Tylenchidae, which can easily be accepted as one of the four families (the others being Atylenchidae, Ecphyadophoridae and Tylodoridae) of the superfamily Tylenchoidea (as is followed here), or in a broader concept can encompass all these groups (as proposed by Raski *et al.*, 1980).

## Family Tylenchidae   rley, 1880

### syn. Boleodoridae Khan, 1964 (Brzeski & Sauer, 1983)

#### Diagnosis

Tylenchoidea. Small to moderately large (0.3–1.3 mm), not abnormally slender or glass fibre-like. No sexual dimorphism in anterior region. Lateral fields each with two, three or four incisures. **Deirids present.** **Prophasmids dorso-sublateral, post-median.** Six inner and four cephalic sensilla present on surface; **cephalic setae absent**; labial disc inconspicuous or absent; a disc-like structure present in *Discotylenchus* and *Cucullitylenchus*. Amphidial aperture on labial plate, extending on lateral side of cephalic region or just postlabial. **Stylet usually weak and slender, small (6–21  $\mu\text{m}$ ),** conus usually less than half total stylet length, rarely with distinct lumen; basal knobs or swellings small, rounded or absent (e.g. *Neopsilenchus*, only subventral knobs absent in *Irantylenchus*); **protractors divergent, not parallel to stylet.** Orifice of dorsal gland close to or at some distance (*Boleodorinae*, *Neothada*) from stylet base. Precorpus cylindrical. Postcorpus or median bulb fusiform or oval, not filling body width, muscular valvate or non-muscular non-valvate, may be not developed. Isthmus slender. Basal bulb with glands, usually pyriform,



abutting intestine, with a cardia at base. Vulva a transverse slit; lateral membranes rarely present (*Aglenchus*). Postvulval uterine sac one body width or less long. Crustaformeria usually a tricolomella, rarely a quadricolomella. Spermatheca offset or partly offset, often elongated and lobe directed anteriorly. Ovary anteriorly outstretched, oocytes usually in a row. Testis outstretched, tip rarely reflexed. Cloacal lips variable in shape; hypopygium present or absent. Spicules small, slender, arcuate. Gubernaculum linear or trough-shaped, fixed. Tails generally filiform, similar in both sexes. **Bursa adanal, simple**, not lobed, rarely absent. **Associates of algae, mosses, lichens and plant roots, but generally not root parasites of any significance.**

#### Type subfamily

Tylenchinae Örley, 1880

#### Other subfamilies

Boleodorinae Khan, 1964

Duosulciinae Siddiqi, 1979

Thadinae Siddiqi, 1986

Tanzaniinae subfam. n.

#### Note

Sakiinae, *Neottolenchus*, *Tenunema* and *Tenunema tenuum* of Tylenchidae are some of the nomina nuda proposed in *Helminthological Abstracts*, Vol. 52 (1983), No. 1511, attributed to an unpublished PhD thesis by S. Kapoor (1983).

#### Key to subfamilies of Tylenchidae

1. Corpus short and broad, about as long as basal bulb ..... **Tanzaniinae**  
Corpus elongate-slender, longer than basal bulb ..... **2**
2. Amphidial apertures prominent, posterior to level of cephalic papillae,  
partially covered by a cuticular flap ..... **Boleodorinae**  
Amphidial apertures rarely prominent, anterior to cephalic papillae, not  
covered by a cuticular flap ..... **3**
3. Lateral field narrow, with a single ridge ..... **Duosulciinae**  
Lateral field broad, with two to three ridges ..... **4**
4. Spermatheca axial; tails short conoid to subcylindroid ..... **Thadinae**  
Spermatheca offset; tails elongate, usually filiform ..... **Tylenchidae**

#### Subfamily Tylenchinae Örley, 1880 (Marcinowski, 1909)

syn. Tylenchini Örley, 1880 (Fuchs, 1937; proposed as the tribe  
name 'Tylenchoidea')

**Aglenchinae Siddiqui & Khan, 1983**

**Dactylotylenchinae Wu, 1969**

#### Diagnosis

Tylenchidae. Body about 0.3–1.3 mm long. Cuticle finely striated, or coarsely annulated (smooth in *Polenchus*). **Lateral fields with three or four incisures.** Amphidial

apertures generally longitudinal slits, but may be ventrally curved, or pore-like. Cephalic region circular in cross-section, finely striated or smooth, continuous or slightly offset. Stylet 6–21  $\mu\text{m}$  long, conus shorter than or rarely as long as shaft, with tip appearing solid; knobs distinct (except *Irantylenchus*). Orifice of dorsal oesophageal gland at about a quarter or less of stylet length behind stylet base. Muscular median oesophageal bulb present or rarely absent (*Sakia*). Basal bulb offset from intestine. Vulval lips simple, or modified (*Aglenchus*). Postvulval uterine sac present (except *Aglenchus*). **Crustaformeria generally a tricolumella. Spermatheca lobed, often offset**, elongated and directed forward. Ovary outstretched, occasionally reflexed at the tip. Testis outstretched, sperm small, rounded. Spicules and gubernaculum typical of the family. Bursa adanal, simple. Tails generally filiform.

#### Type genus

*Tylenchus* Bastian, 1865

#### Other genera

*Aglenchus* Andr ssy, 1954  
*Cervoannulatus* Bajaj, 1997  
*Coslenchus* Siddiqi, 1978  
*Cucullitylenchus* Huang & Raski, 1986  
*Discotylenchus* Siddiqi, 1980  
*Filenchus* Andr ssy, 1954  
*Fraglenchus* gen. n.  
*Irantylenchus* Kheiri, 1972 (Andr ssy, 1976)  
*Polenchus* Andr ssy, 1980  
*Sakia* Khan, 1964

#### Nomina nuda

*Tenunema* Kapoor, 1983  
*Tenunema tenuum* Kapoor, 1983

#### Key to genera of Tylenchinae

1. Median oesophageal bulb absent or represented by a non-muscular swelling without cuticular thickenings ..... *Sakia*  
    Median oesophageal bulb present, muscular, with cuticular thickenings .....2
2. Subventral knobs of stylet absent ..... *Irantylenchus*  
    Subventral knobs of stylet present .....3
3. Cephalic region with a distinct disc-like structure .....4  
    Cephalic region without a disc-like structure .....5
4. Cephalic disc extending laterally as a hood ..... *Cucullitylenchus*  
    Cephalic disc not extending laterally as a hood ..... *Discotylenchus*
5. Cuticle non-annulated on most of body ..... 6  
    Cuticle annulated on most of body ..... 7
6. Head inflated, offset; spicules almost straight; bursa prominent ..... *Cervoannulatus*

- Head continuous with body; spicules arcuate; bursa not prominent ... *Polenchus*
7. Longitudinal ridges outside lateral field present ..... *Coslenchus*  
 Longitudinal ridges outside lateral field absent ..... 8
8. Lateral vulval membranes present; postvulval uterine sac absent ..... 9  
 Lateral vulval membranes absent; postvulval uterine sac present ..... 10
9. Head and body finely annulated; cloacal lips not tubular ..... *Fraglenchus*  
 Head and body coarsely annulated; cloacal lips tubular ..... *Aglenchus*
10. Amphidial apertures straight slits extending along cephalic region;  
 stylet conus shorter than half stylet length ..... *Filenchus*  
 Amphidial apertures pore-like, not extending along cephalic  
 region; stylet conus about half stylet length ..... *Tylenchus*

### Genus *Tylenchus* Bastian, 1865

syn. *Tylelenchus* Bastian, 1865 (= officially rejected name)

*Aerotylenchus* Fotedar & Handoo, 1979

*Areotylenchus* Fortuner, 1984 (junior objective synonym of *Aerotylenchus*)

(Fig. 16, A–I)

### Diagnosis

Tylenchinae. Small to medium sized (0.4–1.3 mm), **ventrally curved upon relaxation**. Cuticle moderately thick (1–2  $\mu\text{m}$ ), distinctly annulated. **Lateral fields each with four incisures**. Prophasmsids dorso-sublateral, postmedian, just behind vulva. Cephalic region continuous, annulated; framework with light or no sclerotization. **Stylet 8–21  $\mu\text{m}$  long, with conus about half (more than one-third) of stylet length**; knobs round or posteriorly sloping. Median oesophageal bulb oval, muscular, anterior to middle of oesophagus; basal bulb pyriform. Cardia distinct. Excretory pore usually opposite basal bulb. Deirids just behind level of excretory pore. Vulva a transverse slit, usually at 60–70% of body length, lips not modified; epiptygma or lateral membranes absent. Vagina generally at right angles to body axis. Postvulval uterine sac about a body width or less long. Spermatheca round to oval, offset. Ovary outstretched. **Tail ventrally arcuate**, often hooked, regularly tapering to a pointed or minutely rounded terminus. Bursa adanal, margins crenate. Spicules cephalated, arcuate, 13–25  $\mu\text{m}$  long. Gubernaculum simple, fixed. Cloacal lips slightly raised, anterior one pointed, posterior usually rounded, **not tubular**. Hypoptygma absent.

### Type species

*Tylenchus davainei* Bastian, 1865 (original spelling *Tylenchus Davainii*)

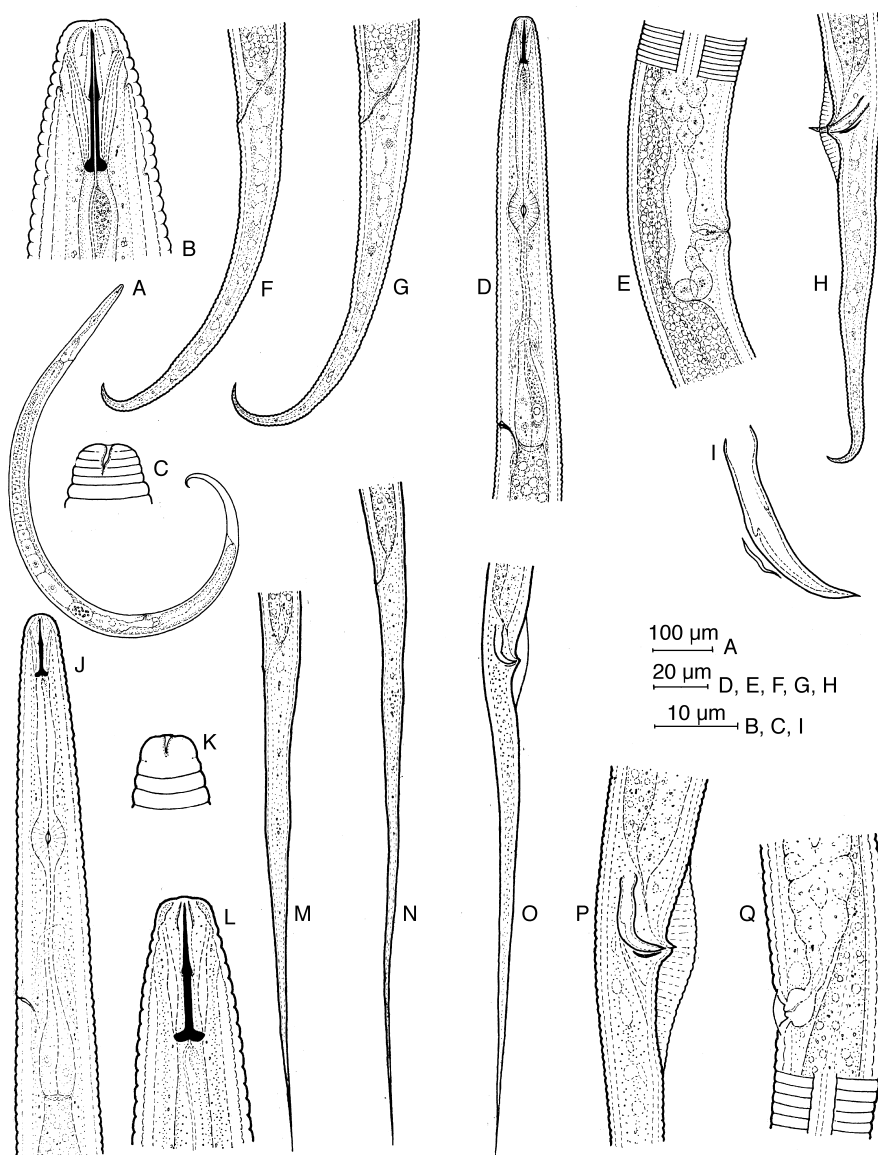
syn. *Anguillulina davainei* (Bastian, 1865) Goodey, 1932

### Other species

*Tylenchus arcuatus* Siddiqi, 1963

*T. barabankensis* Singh & Upadhyay, 1989

*T. bhitaii* Maqbool & Shahina, 1987 (original spelling *bhitai*)



**Fig. 16.** A–I. *Tylenchus davainei* Bastian. J–Q. *Aglenchus agricola* (de Man). A. Female. B and L. Head ends of females. C and K. Cephalic regions showing amphidial apertures. D & J. Oesophageal regions of females. E and Q. Vulval regions. F, G, M and N. Tail ends of females. H and O. Tail ends of males. I. Spiculum and gubernaculum. P. Spicular region. (A–I. After Andr  ssy, 1977; J–Q. After Andr  ssy, 1980.)

- T. capitatus* Andrassy, 1979 (syn. of *T. elegans* for Brzeski, 1996a)  
*T. elegans* de Man, 1876  
     syn. *T. davainei* apud Thorne & Malek, 1968  
     *T. davainei* apud Szczygieł, 1969  
*T. faizabadensis* Singh & Upadhyay, 1989  
*T. hayati* Khan, 1985  
*T. kashmirensis* Mahajan, 1973  
*T. kirjanovae* Andrassy, 1954  
     syn. *T. uncinatus* Kirjanova, 1954; nec *T. uncinatus* Fuchs, 1929 (Aphelenchida)  
*T. madarpurensis* Sultan, Singh & Sakhuja, 1991  
*T. magnus* Khurma & Gupta, 1988  
*T. maius* Andrassy, 1979  
*T. martini* Zell, 1988 (syn. of *T. davainei* for Brzeski, 1996a)  
*T. naranensis* Maqbool, Zarina & Ghazala, 1987  
*T. neoandrassyi* Geraert & Raski, 1987 (was a nom. nov.)  
     syn. *T. andrassyi* Fotedar & Kaul, 1985; nec *T. andrassyi* Szczygieł, 1969  
*T. neodavainei* Wu, 1969  
*T. pakistanensis* Farooq, Fatima & Khan, 1991  
*T. parangalici* Katalan-Gateva & Aleksiev, 1990 (sp. inq. for Brzeski, 1996a)  
*T. rex* Andrassy, 1979  
*T. ritae* Siddiqi, 1963 (syn. of *T. elegans* for Brzeski, 1996a)  
*T. rohtangus* Khan, 1985  
*T. safroni* (Fotedar & Handoo, 1979) Siddiqi, 1986  
     syn. *Aerotylenchus safroni* Fotedar & Handoo, 1979  
*T. sherianus* Andrassy, 1981 (was a nom. nov.)  
     syn. *T. sheri* Andrassy, 1979 (= primary homonym of *T. sheri* Khan & Khan, 1978)  
*T. skarduensis* Maqbool & Shahina, 1987  
*T. stachys* Brzeski, 1996  
*T. stylolineatus* Wu, 1969  
*T. subdavainei* Mukhina, 1981  
*T. tortus* Andrassy, 1979

#### Species inquirendae et incertae sedis

- Tylenchus cobbi* de Man, 1907  
*T. davainei* var. *gracilis* Rahm, 1928  
     syn. *T. gracilis* Rahm, 1928 (= junior primary homonym of *T. gracilis* de Man, 1880, became *T. rahmi* Fortuner, 1985)  
*T. exiguus* de Man, 1876  
     syn. *Anguillulina exigua* (de Man) Goodey, 1932  
     *Filenchus exiguus* (de Man) Ebsary, 1991  
*T. farwicki* Rahm, 1925  
     syn. *Anguillulina farwicki* (Rahm) Goodey, 1932  
     *Filenchus farwicki* (Rahm) Ebsary, 1991  
*T. filiformis* f. *parvus* Micoletzky, 1922  
*T. foliicola* Zimmermann, 1903  
     syn. *Filenchus foliicola* (Zimmermann) Ebsary, 1991

- T. gracilis* Cobb, 1888 (= junior primary homonym of *T. gracilis* de Man, 1880)  
 syn. *Aphelenchus gracilis* (Cobb, 1888) Cobb, 1891  
*T. incisa* (Rahm, 1938) Siddiqi, 1986  
 syn. *Anguillulina* (*Tylenchus*) *incisa* Rahm, 1938  
*T. intactus* Kirjanova, 1951  
*T. kreisi* Fortuner, 1985 (nom. nov. for *T. exiguus* Kreis, 1924)  
*T. leontopodii* Örley, 1880  
 syn. *Anguillulina* sp., apud Frauenfeld, 1872  
*T. (Lelenchus) micoletzkyi* Andrásy, 1954  
 syn. *Tylenchus* sp. in Micoletzky, 1922  
*Lelenchus micoletzkyi* (Andrásy) Baker, 1962  
*Filenchus micoletzkyi* (Andrásy) Ebsary, 1991  
*T. minimus* Rahm, 1925  
 syn. *Anguillulina minima* (Rahm) Goodey, 1932  
*Filenchus minimus* (Rahm) Ebsary, 1991  
*T. minor* Xie & Feng, 1997  
*T. minutus* Cobb, 1893  
 syn. *Anguillulina minuta* (Cobb) Goodey, 1932  
*Lelenchus minutus* (Cobb) Meyl, 1961  
*Filenchus minutus* (Cobb) Siddiqi, 1986  
*T. nivalis* Kühn, 1880  
*T. paraminor* Xie & Feng, 1997  
*T. pillulifer* Von Linstow, 1877 (perhaps not a Tylenchida, see Loof, 1961)  
 syn. *Anguillulina pillulifer* (Von Linstow) Goodey, 1932  
*T. stylohus* Xie & ZhiXin, 1995  
*T. terricola* Bastian, 1865  
 syn. *Anguillulina terricola* (Bastian) Goodey, 1932  
*Filenchus terricola* (Bastian) Ebsary, 1991  
*T. tiliac* Örley, 1880  
*T. turbo* Marcinowski, 1909 (? = juvenile of *Ditylenchus*)  
 syn. *Anguillulina turbo* (Marcinowski) Goodey, 1932  
*Filenchus turbo* (Marcinowski) Ebsary, 1991  
*T. uniformis* Cobb, 1893  
 syn. *Anguillulina uniformis* (Cobb) Goodey, 1932  
*Filenchus uniformis* (Cobb) Ebsary, 1991  
*T. weidenbachi* Rahm, 1925  
 syn. *Anguillulina weidenbachi* (Rahm) Goodey, 1932  
*T. yanchiapingensis* (Rahm, 1937) Siddiqi, 1986  
 syn. *Anguillulina yanchiapingensis* Rahm, 1937

#### Nomina nuda

- Tylenchus* (*Aglenchus*) *annulatus* Bello, 1969  
*Tylenchus* *serenus* Kapoor, 1983  
*T. varicaudatus* Kapoor, 1983  
*T. vividus* Kapoor, 1983

## Remarks

The identity of *Tylenchus davainei* is doubtful. Bastian (1865) sketched straight conoid tails for female and male, which is contrary to the present concept of the genus. The sharply conical male tail with a large bursa and flattened cap-like head, as illustrated by Bastian (1865), are reminiscent of those of *Ditylenchus dipsaci*. Andr ssy (1977) discussed in detail the status of *T. davainei* and of the genus *Tylenchus*.

The genus *Aerotylenchus* Fotedar & Handoo, 1979, proposed for *A. safroni* (type species) from Kashmir, India, cannot be differentiated from the genus *Tylenchus* and is here considered a junior synonym of it. Fortuner (1984a) argued that in the original publication of *Aerotylenchus* there was clear evidence of an inadvertent error (*vide* ICZN Article 32 (c) (ii)) since the authors did not mean to call their nematode 'a flying *Tylenchus*', and, therefore, he proposed the name *Areotylenchus* to replace it. I consider *Aerotylenchus* as the correct original spelling, being based on the *aerolation* as used there and by other workers for the lateral fields. The word *aerolation* is consistently used to describe the lateral fields in the diagnosis, abstract and relationship of the genus as on page 145 by Fotedar & Handoo (1979) and there is no clear evidence in the original description of an inadvertent error. The name cannot be rejected because of inappropriateness (Article 18). Thus Fortuner's action is considered an unjustified emendation (*vide* ICZN Article 33 (b) (iii)), and the emended name he proposed, i.e. *Areotylenchus* Fortuner, 1984, becomes a junior objective synonym of *Aerotylenchus*.

ETYMOLOGY. Greek *tylos* = a knot, knob, and *enchos* = a spear.

The type species was found by Bastian (1865) in a sheet of moss covering a large boulder lying in a freshwater stream at Falmouth, England. Keys to *Tylenchus* spp. are given by Andr ssy (1979a) and Maqbool and Shahina (1987).

**Genus *Filenchus* Andr ssy, 1954 (Meyl, 1961)**

**syn. *Tylenchus* (*Filenchus* Andr ssy, 1954)**

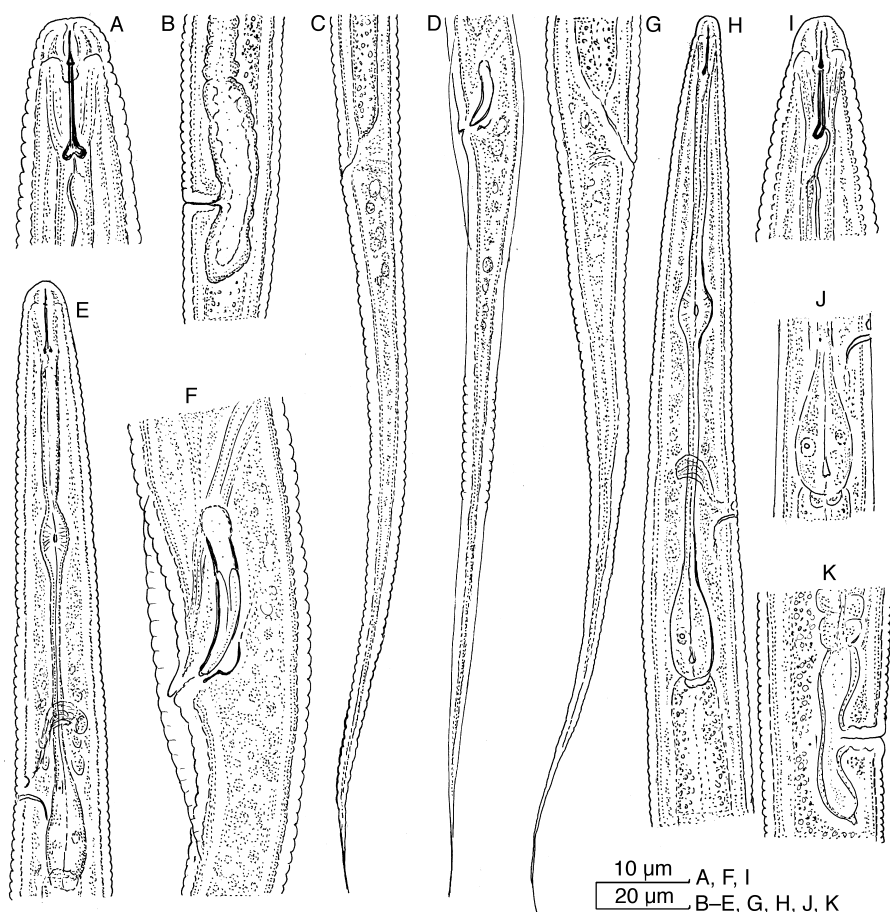
***Dactylotylenchus* Wu, 1968**

***Lambertia* Brzeski, 1977**

(Fig. 17, A–F)

## Diagnosis

Tylenchinae. Body small to moderately large (0.3–1.3 mm), straight to arcuate when relaxed. Cuticle with fine to moderately coarse annulation. Lateral fields each with four incisures, wider than one-sixth of body width. Deirids present. Cephalic region broadly rounded or conoid-rounded, rarely truncate, continuous or slightly offset, finely annulated; labial plate squarish or four-lobed, with four cephalic sensilla pits near edge of each lobe; labial disc inconspicuous, small, bearing six labial sensilla around oral opening. **Amphidial apertures straight longitudinal slits or clefts, beginning from edge of labial plate and occupying whole of cephalic lateral sides.** Cephalic framework of six equal sectors, with light to moderate sclerotization. Stylet feeble or moderately developed, generally 7–15  $\mu\text{m}$  long; **conus** solid-appearing anteriorly, sharply pointed, **about one-third of total stylet length**; knobs distinct,



**Fig. 17.** A–F. *Filenchus uliginosus* (Brzeski) (= *Lambertia uliginosa* Brzeski), paratypes. G–K. *Irantylenchus clavidorus* Kheiri, paratypes. A and I. Head ends of females. B and K. Vulval regions. C and G. Tail ends of females. D. Tail end of male. E and H. Oesophagus of females. F. Spicular region. J. Basal region of oesophagus of female.

rounded, often closely adpressed to the shaft. Orifice of dorsal gland close behind stylet base. Median bulb oval to rounded, muscular, valvate. Basal bulb offset from intestine, generally pyriform. Cardia distinct. Vulva at about 55–70%; lips not modified; lateral membranes absent. Vagina directed inward. Spermatheca offset, usually lobe-like and directed forward. Ovary outstretched, mostly with a single row of oocytes. Rectum and anus distinct. **Tails generally filiform and straight**, may be elongate-conoid and slightly ventrally arcuate **but not hooked**. Bursa adanal. **Spicules tylenchoid, robust, with internal thickening, generally angular in posterior half, tip pointed**. Gubernaculum generally strongly cupped. Anterior lip of cloaca pointed, posterior lip generally rounded.



## Type species

- Filenchus filiformis* (Bütschli, 1873) Meyl, 1961  
 syn. *Tylenchus filiformis* Bütschli, 1873  
*Anguillulina filiformis* (Bütschli) Goodey, 1932  
*Filenchus filiformis* (Bütschli) Ebsary, 1991  
*Tylenchus vulgaris* Brzeski, 1963 (= *T. filiformis* apud Andrassy (1954), see remarks below)  
*F. vulgaris* (Brzeski) Lownsbery & Lownsbery, 1985  
*F. vulgaris* (Brzeski) Mizukubo & Minagawa, 1986 (combination proposed earlier)  
*Tylenchus (Lelenchus) mirus* Husain & Khan, 1967  
*F. mirus* (Husain & Khan) Siddiqi, 1986 (syn. of *F. vulgaris* for Brzeski, 1997)  
*F. mirus* (Husain & Khan) Raski & Geraert, 1986  
*Tylenchus (Lelenchus) cynodontus* Husain & Khan, 1967  
*F. cynodontus* (Husain & Khan) Siddiqi, 1986 (syn. of *F. vulgaris* for Brzeski, 1997)  
*F. cynodontus* (Husain & Khan) Raski & Geraert, 1986  
*Tylenchus (Filenchus) ruatus* Egunjobi, 1967  
*F. ruatus* (Egunjobi, 1967) Siddiqi, 1986  
*Malenchus ruatus* (Egunjobi) Sultan, Singh & Sakhuja, 1991  
*F. conicephalus* Siddiqui & Khan, 1983 (syn. of *F. vulgaris* for Raski & Geraert, 1987)

## Other species

- Filenchus afghanicus* (Khan & Khan, 1978) Siddiqi, 1986  
 syn. *Tylenchus afghanicus* Khan & Khan, 1978  
*F. afghanicus* (Khan & Khan) Sultan, 1986  
*F. afghanicus* (Khan & Khan) Raski & Geraert, 1987 (unjustified transfer)  
*F. altherri* (Fortuner, 1985) Siddiqi, 1986  
 syn. *Tylenchus altherri* Fortuner, 1985 (was a nom. nov.)  
*Anguillulina (Tylenchus) aberrans* Altherr, 1952 (= junior primary homonym of *Anguillulina aberrans* Thorne, 1935)  
*Tylenchus (Lelenchus) aberrans* (Altherr) Andrassy, 1954  
*Lelenchus aberrans* (Altherr) Baker, 1962  
*F. andrassyi* (Szczygieł, 1969) Andrassy, 1979  
 syn. *Tylenchus andrassyi* Szczygieł, 1969  
*F. pseudoorbis* Mukhina, 1981 (syn. by Brzeski, 1997)  
*F. angusticephalus* (Thorne & Malek, 1968) Siddiqi, 1986 (syn. of *F. thornei* for Raski & Geraert, 1987; syn. of *F. vulgaris* for Brzeski, 1997)  
 syn. *Tylenchus angusticephalus* Thorne & Malek, 1968  
*F. annulatus* (Siddiqui & Khan, 1983) Siddiqi, 1986 (syn. of *F. misellus* for Brzeski, 1997)  
 syn. *Lelenchus annulatus* Siddiqui & Khan, 1983  
*F. annulatus* (Siddiqui & Khan) Raski & Geraert, 1986  
*F. aquilonius* (Wu, 1969) Lownsbery & Lownsbery, 1985 (syn. of *F. orbis* for Brzeski, 1997)

- syn. *Tylenchus aquilonius* Wu, 1969  
*F. aquilonius* (Wu, 1969) Siddiqi, 1986
- F. australis* Xie & Feng, 1996
- F. balcarceanus* Torres & Geraert, 1996
- F. baloghi* (Andrássy, 1958) Siddiqi, 1986  
 syn. *Tylenchus* (*Tylenchus*) *baloghi* Andrásy, 1958
- F. brevis* Lal & Khan, 1988 (syn. of *F. vulgaris* for Brzeski, 1997)
- F. butteus* (Thorne & Malek, 1968) Raski & Geraert, 1987  
 syn. *Tylenchus butteus* Thorne & Malek, 1968  
*Tylenchus cylindricollis* Thorne & Malek, 1968  
*F. cylindricollis* (Thorne & Malek) Siddiqi, 1986 (syn. by Brzeski, 1997)  
*Tylenchus plattensis* Thorne & Malek, 1968  
*F. plattensis* (Thorne & Malek) Siddiqi, 1986 (syn. by Brzeski, 1997)
- F. capsici* Xie & Feng, 1996
- F. clarki* (Egunjobi, 1968) Siddiqi, 1986  
 syn. *Tylenchus clarki* Egunjobi, 1968  
*F. clarki* (Egunjobi) Raski & Geraert, 1986
- F. compositus* (Eroshenko, 1971) Siddiqi, 1986  
 syn. *Tylenchus* (*Filenchus*) *compositus* Eroshenko, 1971
- F. crassacuticulus* (Wu, 1968) Andrásy, 1976  
 syn. *Dactylotylenchus crassacuticulus* Wu, 1968  
*T. crassacuticulus* (Wu) Bello, 1972  
*F. crassacuticulus* (Wu) Siddiqi, 1986
- F. crassus* (Siddiqui & Khan, 1983) Siddiqi, 1986 (syn. of *F. misellus* for Brzeski, 1997)  
 syn. *Lelenchus crassus* Siddiqui & Khan, 1983  
*F. crassus* (Siddiqui & Khan) Raski & Geraert, 1986
- F. criniformicaudatus* (Kazachenko, 1975) Siddiqi, 1986  
 syn. *Lelenchus criniformicaudatus* Kazachenko, 1975  
*F. criniformicaudatus* (Kazachenko) Raski & Geraert, 1986  
*F. criniformicaudatus* (Kazachenko) Sultan, 1986
- F. cylindricauda* (Wu, 1969) Siddiqi, 1986 (syn. of *F. thornei* for Brzeski, 1997)  
 syn. *Tylenchus cylindricaudus* Wu, 1969
- F. cylindricus* (Thorne & Malek, 1968) Niblack & Bernard, 1985 (syn. of *F. thornei* for Brzeski, 1997)  
 syn. *Tylenchus cylindricus* Thorne & Malek, 1968  
*Ottolenchus cylindricus* (Thorne & Malek) Siddiqi & Hawksworth, 1982  
*Tylenchus hageni* Elmiligy, 1971  
*F. hageni* (Elmiligy) Siddiqi, 1986 (syn. of *F. cylindricus* for Raski & Geraert, 1987)
- F. elegantulus* Raski & Geraert, 1987
- F. filipjevi* Andrásy, 1988 (syn. of *F. thornei* for Brzeski, 1997)
- F. goodeyi* (Das, 1960) Siddiqi, 1986  
 syn. *Tylenchus* (*Filenchus*) *goodeyi* Das, 1960
- F. hamatus* (Thorne & Malek, 1968) Raski & Geraert, 1987  
 syn. *Tylenchus hamatus* Thorne & Malek, 1968
- F. hazenensis* (Wu, 1969) Andrásy, 1976

- syn. *Tylenchus hazenensis* Wu, 1969  
*F. hazenensis* (Wu) Siddiqi, 1986  
*Dactylotylenchus filiformis* Wu, 1968  
*F. filiformis* (Wu) Siddiqi, 1986 (= secondary homonym of *F. filiformis* (Bütschli) Meyl, 1961)  
*Tylenchus neofiliformis* Bello, 1971 (was a nom. nov. for *T.* (= *Dactylotylenchus*) *filiformis*, nec *T. filiformis* Bütschli, 1973)  
*F. neofiliformis* (Bello) Siddiqi, 1986
- F. heterocephalus* Xie & Feng, 1996  
*F. hongkongensis* Xie & Feng, 1996  
*F. infirmus* (Andrássy, 1954) Meyl, 1961  
 syn. *Tylenchus (Lelenchus) infirmus* Andrásy, 1954  
*Lelenchus infirmus* (Andrássy) Meyl, 1961  
*Anguillulina leptosoma* f. *minuta* Andrásy, 1952  
*F. minutus* (Andrássy, 1952) Andrásy, 1972  
 (= secondary homonym of *F. minutus* Cobb, 1893)
- F. istvani* Zell, 1988 (was a nom. nov. for *Tylenchus (Lelenchus) minutus* Cobb, 1893 apud Andrásy, 1954)
- F. japonicus* Mizukubo & Minagawa, 1986 (syn. of *F. thornei* for Brzeski, 1997)  
 syn. *Malenchus japonicus* (Mizukubo & Minagawa, 1986) Sultan, Singh & Sakhuja, 1991
- F. longicaudatulus* Zell, 1988  
*F. longicaudatus* Sultan, Singh & Sakhuja, 1991
- F. magnus* (Husain & Khan, 1976) Siddiqi, 1986 (syn. of *F. misellus* for Brzeski, 1997)  
 syn. *Lelenchus magnus* Husain & Khan, 1976  
*F. magnus* (Husain & Khan) Raski & Geraert, 1986
- F. marinus* (Timm, 1956) Raski & Geraert, 1987  
 syn. *Tylenchus marinus* Timm, 1956
- F. microdorus* (Chawla, Prasad, Khan & Nand, 1969) Siddiqi, 1986 (syn. of *F. misellus* for Brzeski, 1997)  
 syn. *Tylenchus (Lelenchus) microdorus* Chawla, Prasad, Khan & Nand, 1969  
*F. microdorus* (Chawla et al.) Raski & Geraert, 1986
- F. misellus* (Andrássy, 1958) Raski & Geraert, 1987  
 syn. *Ditylenchus misellus* Andrásy, 1958  
*Tylenchus ditissimus* Brzeski, 1963  
*F. ditissimus* (Brzeski) Siddiqi, 1986  
*Tylenchus parvissimus* Thorne & Malek, 1968  
*F. parvissimus* (Thorne & Malek) Siddiqi, 1986 (syn. by Brzeski, 1997)  
*Tylenchus neominimus* Savkina, 1989 (sp. inq. for Brzeski, 1996; syn. by Brzeski, 1997)  
*F. amaritus* Zell, 1988 (syn. by Brzeski, 1997)
- F. obtusicaudatus* (Erzhanov, 1964) Siddiqi, 1986  
 syn. *Tylenchus obtusicaudatus* Erzhanov, 1964
- F. orbus* (Andrássy, 1954) Meyl, 1961  
 syn. *Tylenchus (Filenchus) orbus* Andrásy, 1954
- F. polyhypnus* (Steiner & Albin, 1946) Meyl, 1961  
 syn. *Tylenchus polyhypnus* Steiner & Albin, 1946

- F. prelli* Rühm, 1956  
 syn. *Tylenchus prelli* (Rühm) Brzeski, 1968  
*Tylenchus prelli* (Rühm) Bello, 1972
- F. quartus* (Szczygieł, 1969) Siddiqi, 1986  
 syn. *Tylenchus quartus* Szczygieł, 1969  
*F. quartus* (Szczygieł) Sultan, 1986
- F. resistens* Zell, 1988
- F. retusus* (Kazachenko, 1975) Siddiqi, 1986  
 syn. *Lelenchus retusus* Kazachenko, 1975  
*F. retusus* (Kazachenko) Raski & Geraert, 1986
- F. sandneri* (Wasilewska, 1965) Raski & Geraert, 1987  
 syn. *Tylenchus sandneri* Wasilewska, 1965  
*Tylenchus cerealis* Kheiri, 1970  
*F. cerealis* (Kheiri) Raski & Geraert, 1987
- F. sheri* (Khan & Khan, 1978) Siddiqi, 1986 (syn. of *F. misellus* for Brzeski, 1997)  
 syn. *Tylenchus sheri* Khan & Khan, 1978  
*F. sheri* (Khan & Khan) Sultan, 1986
- F. sindhicus* Shahina & Maqbool, 1994
- F. spiculatus* Sultan, 1986
- F. striatus* (Das, 1960) Siddiqi, 1986  
 syn. *Tylenchus* (*Filenchus*) *striatus* Das, 1960  
*F. striatus* (Das) Sultan, 1986
- F. tenuis* (Siddiqui & Khan, 1983) Siddiqi, 1986  
 syn. *Lelenchus tenuis* Siddiqui & Khan, 1983  
*F. tenuis* (Siddiqui & Khan) Raski & Geraert, 1986
- F. teres* (Eroshenko, 1971) Siddiqi, 1986  
 syn. *Tylenchus* (*Lelenchus*) *teres* Eroshenko, 1971  
*F. teres* (Eroshenko) Raski & Geraert, 1986
- F. terrestris* Raski & Geraert, 1987
- F. thornei* (Andrássy, 1954) Andrásy, 1963  
 syn. *Tylenchus* (*Aglenchus*) *thornei* Andrásy, 1954  
*Aglenchus thornei* (Andrássy) Meyl, 1961
- F. uliginosus* (Brzeski, 1977) Siddiqi, 1986  
 syn. *Lambertia uliginosa* Brzeski, 1977  
*F. uliginosus* (Brzeski) Raski & Geraert, 1987
- F. valkanovi* (Andrássy, 1958) Meyl, 1961  
 syn. *Tylenchus* (*Filenchus*) *valkanovi* Andrásy, 1958  
*Ditylenchus valkanovi* (Andrássy) Zell, 1988
- F. zaphari* (Mavlyanov, 1976) Siddiqi, 1986 (syn. of *F. misellus* for Brzeski, 1997)  
 syn. *Tylenchus* (*Lelenchus*) *zaphari* Mavlyanov, 1976  
*F. zaphari* (Mavlyanov) Raski & Geraert, 1986

## Remarks

The original description of the type species of the genus *Filenchus*, viz. *T. filiformis* Bütschli, 1873, is insufficient to characterize the genus *Filenchus* and to differentiate it from related genera (e.g. *Ottolenchus*). The prevalent concept of the genus at the time of its proposal or at the elevation of its rank was based on a well-annulated

body and straight filiform tail, and not on the number of incisures in the lateral fields (cf. *Ottolenchus*) or the form of the amphid, spermatheca, etc. Invoking Article 70(a) of the ICZN, I assume that Andrassy (1954) correctly identified *T. filiformis*, which he redescribed at the time of its designation as type species of *Filenchus*, and that, according to the now prevailing concept of the genus, *T. filiformis* Bütschli, 1873 had four incisures in the lateral fields and longitudinal amphidial apertures.

*Filenchus* was considered to be a junior synonym of *Tylenchus* by many workers (Thorne & Malek, 1968; Bello, 1971; Golden, 1971), while upheld as valid by many others (Goodey, 1963; Siddiqi, 1971; Andrassy, 1976, 1979). Andrassy's (1979a) revision of the genus *Tylenchus* restricts it to 15 species and excludes others. Andrassy (1976) synonymized *Lelenchus* Andrassy with *Filenchus*, but as discussed above, *Lelenchus* is regarded here as a valid genus. The genera *Dactylotylenchus* Wu and *Lambertia* Brzeski were considered by Siddiqi (1986) as junior synonyms of *Filenchus*.

*Filenchus*, *Irantylenchus*, *Discotylenchus* and *Cucullitylenchus* are the only genera in Tylenchinae which have amphids with a straight longitudinal slit occupying most of the cephalic region height. It is possible that some of the *Filenchus* spp. listed above may need transferring to other genera, e.g. *Sakia*, *Basiria* and *Ottolenchus*, after the structure of the amphid, oesophagus and lateral field have been restudied.

ETYMOLOGY. *Fil* from first letters of its type species name *filiformis*, and *enchus* from *Tylenchus*.

The type species (female) was found by Bütschli (1873) under moss in Germany.

### **Genus *Irantylenchus* Kheiri, 1972 (Andrassy, 1976)**

**syn. *Tylenchus* (*Irantylenchus* Kheiri, 1972)**

(Fig. 17, G–K)

#### **Diagnosis**

Tylenchinae. Body about 1 mm or less long, straight to slightly arcuate upon relaxation. Cuticle finely annulated. Lateral fields each with four incisures, mostly not areolated. Deirids opposite excretory pore. Amphids with longitudinal slit-like apertures. Cephalic region elevated, rounded, continuous, finely striated. **Stylet with a clavate base**, 11–12  $\mu\text{m}$  long in type species; conus small (about one-third of its total length); usual three basal knobs lacking, the clavate basal swelling more developed on dorsal side, perhaps representing the dorsal knob. Oesophageal lumen joins the stylet lumen on the ventral side of the clavate stylet base in type species. **Orifice of dorsal gland half to one stylet length from stylet base**. Median bulb muscular, valvate. Basal bulb pyriform, with distinct cardia. Vulva a transverse slit, at 62–65% of body length. Postvulval uterine sac shorter than body width. Spermatheca offset, elongated. Ovary outstretched. Prothasms dorso-sublateral, near vulva. Rectum and anus distinct. Tail elongate-filiform. Bursa adanal. Anterior cloacal lip pointed, posterior one rounded. Spicules pointed, 21–33  $\mu\text{m}$  long in type species. Gubernaculum trough-like, 5–6  $\mu\text{m}$  long in type species.

## Type species

*Irantylenchus clavidorus* Kheiri, 1972

syn. *Tylenchus* (*Irantylenchus*) *clavidorus* Kheiri, 1972; syn. of *T. vicinus*

## Present status

*Irantylenchus vicinus* (Szczygieł, 1970) Sumenkova, 1984

syn. *Tylenchus vicinus* Szczygieł, 1970

*Tylenchus* (*Irantylenchus*) *clavidorus* Kheiri, 1972

*Irantylenchus clavidorus* Kheiri, 1972

## Remarks

*Irantylenchus* was proposed as a subgenus of *Tylenchus* without designation of a type species, but *Tylenchus* (*Irantylenchus*) *clavidorus* becomes type by monotypy (ICZN Article 68(d)). Andrassy (1976) raised the subgenus to genus rank, thereby enacting the transfer of its species. However, Kheiri (1972) used the subgeneric name in apposition to species name, and he is deemed to have transferred the species to *Irantylenchus*. Sumenkova (1984) gave a diagnosis of the genus.

ETYMOLOGY. From Iran, country of type species and of author, and *Tylenchus*.

The type species was found around roots of alfalfa (*Medicago sativa* L.) in an orchard at Isfahan, Iran.

**Genus *Discotylenchus* Siddiqi, 1980**

(Fig. 18)

## Diagnosis

Tylenchinae. Small sized (under 1 mm), straight to C-shaped upon relaxation. Cuticle finely annulated. Lateral fields each with four incisures, not areolated. Cephalic region markedly tapering, smooth, **with an offset, distinct perioral disc**; framework lightly sclerotized. **Amphids longitudinal slits at base of perioral disc**. Deirids present. Prothasms postmedian, in female in or close to vulval region. Stylet slender, under 10 µm long, with minute basal knobs. Orifice of dorsal gland close to stylet base. Median bulb oval, muscular, valvate. Basal bulb saccate, offset from intestine. Cardia round or discoidal. Vulva at about 60–70% of body length. Postvulval uterine sac short. Spermatheca offset, lobed. Ovary short, outstretched, with oocytes in a row. Tail elongate-filiform finely pointed or rounded, not arcuate ventrally. Bursa adanal. Spicules 11–13 µm long in type species. Gubernaculum small (3–5 µm long).

## Type species

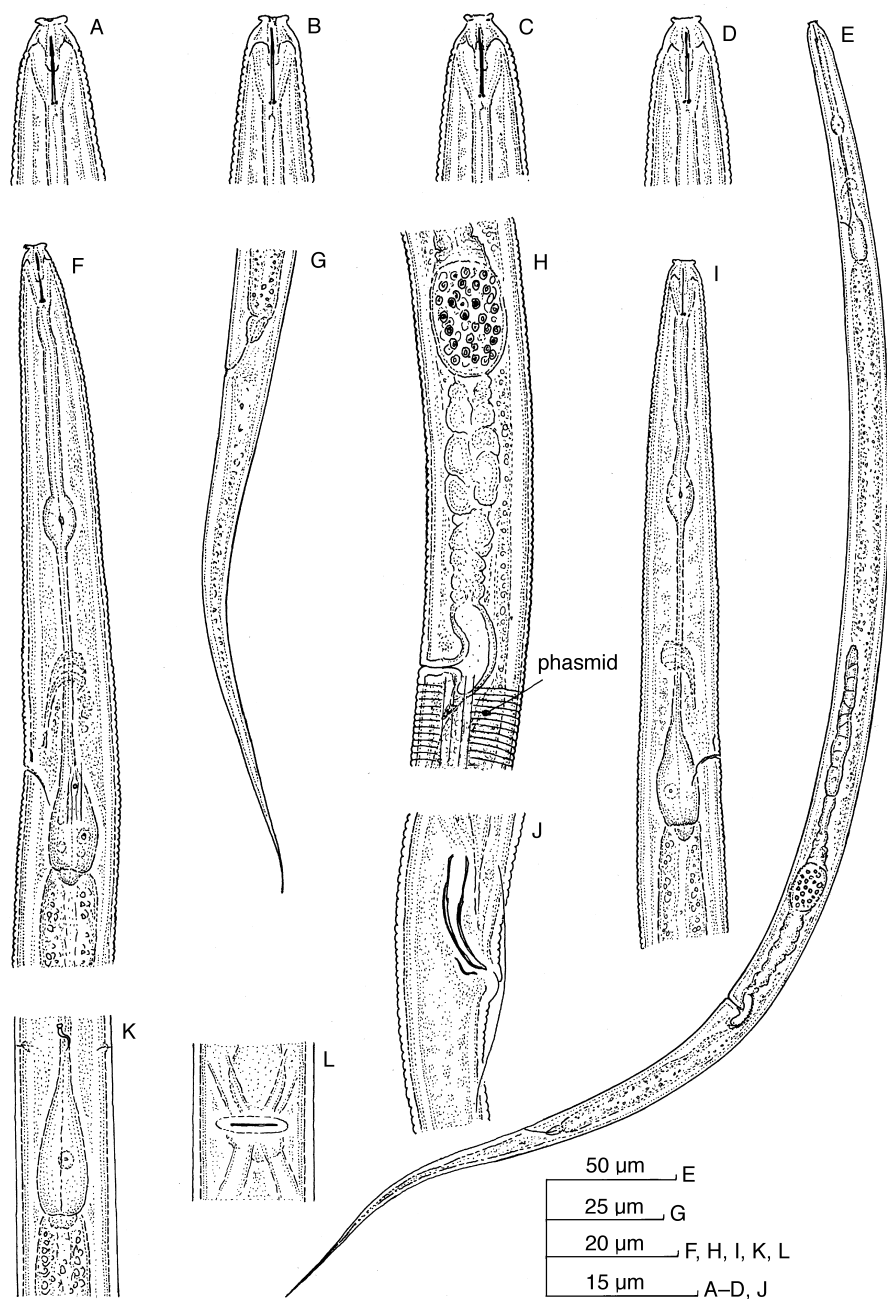
*Discotylenchus discretus* Siddiqi, 1980

syn. *Filenchus discretus* (Siddiqi) Raski & Geraert, 1987

## Other species

*Discotylenchus attenuatus* Siddiqi, 1980

syn. *Filenchus attenuatus* (Siddiqi) Raski & Geraert, 1987



**Fig. 18.** *Discotylenchus discretus* Siddiqi. D and J. Males; remainder females. A–D. Head ends. E. Entire female. F and I. Oesophageal regions. G. Tail. H. Vulval region. J. Spicular region. K. Basal region of oesophagus showing excretory pore and deirids in ventral view. L. Vulva in ventral view. (After M.R. Siddiqi (1980), courtesy Helminthological Society of Washington.)

- D. azadkashmirensis* (Maqbool & Shahina, 1985) Siddiqi & Lal, 1992  
syn. *Ottolenchus azadkashmirensis* Maqbool & Shahina, 1985
- D. brevicaudatus* Brzeski, 1986  
syn. *Filenchus brevicaudatus* (Brzeski) Raski & Geraert, 1987
- D. discolabialis* (Mizukubo, 1993) comb. n.  
syn. *Filenchus discolabialis* Mizukubo, 1993
- D. longicauda* (Maqbool & Shahina, 1985) Siddiqi & Lal, 1992  
syn. *Ottolenchus longicauda* Maqbool & Shahina, 1985

#### Note

Amphid apertures in *D. discolabialis* are longitudinal but slightly sinuate extending down to base of stylet or 6  $\mu\text{m}$  from anterior end. *Cucullitylenchus* Huang & Raski, 1986 is very similar to *Discotylenchus* and further studies are needed particularly on the structure of the cephalic region and amphidial apertures of *Discotylenchus* to decide if the two genera are synonymous. I have seen longitudinal slit-like amphidial apertures extending for a short distance from the labial disc in *Discotylenchus*. Scanning electron microscopy study of *Discotylenchus* head would make it clear if a hood-like structure similar to *Cucullitylenchus* is also present in this genus.

ETYMOLOGY. From Greek *diskos* = disc (for labial disc), and *Tylenchus*.

The type species was found around apple and cabbage roots in Damascus, Syrian Arab Republic.

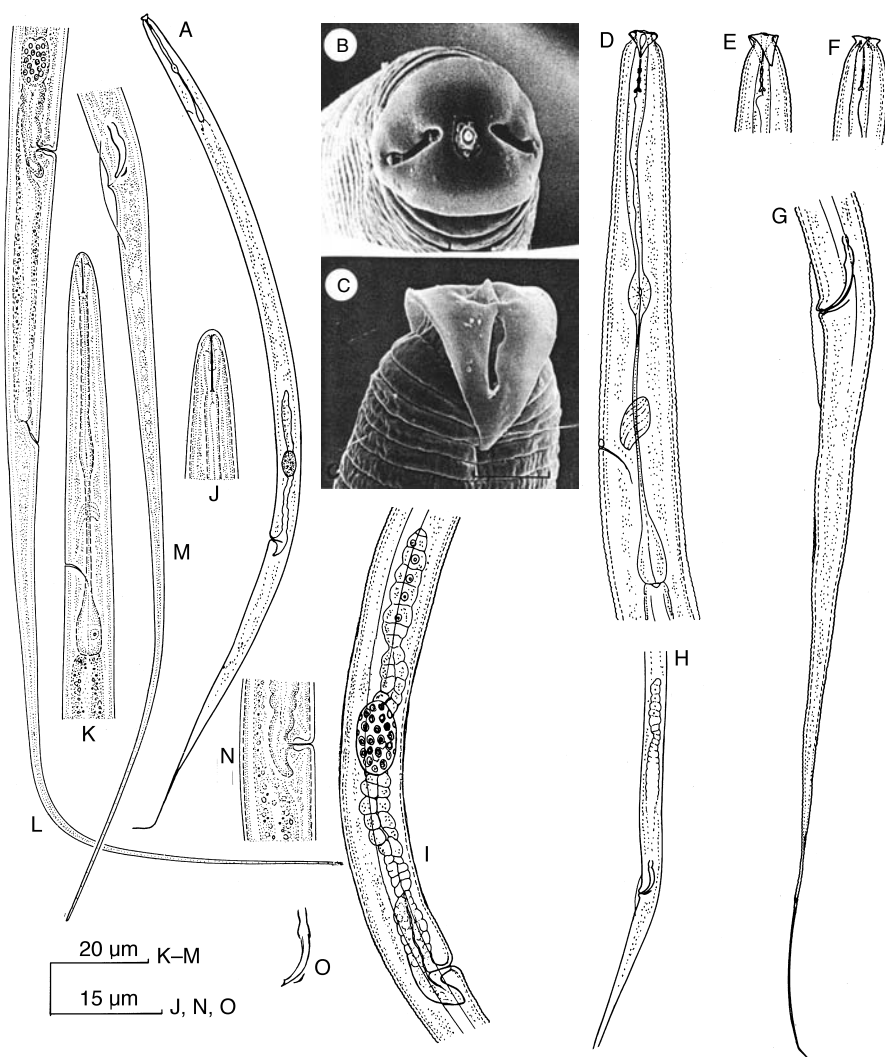
#### Genus *Cucullitylenchus* Huang & Raski, 1986

(Fig. 19, A–I)

#### Diagnosis

Tylenchinae. Body slender, under 0.6 mm long, almost straight upon relaxation. Cuticle thin, finely striated. Lateral field a wide (more than 3  $\mu\text{m}$ ) band marked by two distinct incisures, inner two incisures, sometimes more, seen in SEM. Cephalic region set off from body, with a **labial disc extending laterally on either sides as V-shaped structures to three or four body annules and bearing elongate, longitudinal, slit-like amphidial apertures**. Stylet small, delicate, 5–9  $\mu\text{m}$  long in type species; conus amalgamated with shaft but appears shorter than it; basal knobs small, rounded. Orifice of dorsal gland just behind stylet base in type species. **Median bulb oval, weakly muscular, with minute inner thickenings**, at about middle of oesophagus. Isthmus elongate-slender. Basal bulb small, pyriform, offset from intestine. **Cardia small, rounded**. Excretory pore behind nerve ring which crosses isthmus near its middle; excretory canal sclerotized. Vulva a transverse slit, at 61–66% in type species; lips not modified; lateral membranes indistinct. Ovary outstretched, oocytes in a single file. Spermatheca bi- or trilobed. **Crustaformeria a quadricolumella**. Postvulval uterine sac less than one body width long. Tails similar between sexes, elongate filiform ( $c = 2.9\text{--}6.6$ ), terminus finely drawn out in type species. Bursa adanal. Spicules cephalated, ventrally arcuate, 12–16  $\mu\text{m}$  long in type species. Gubernaculum trough-shaped, 4–6  $\mu\text{m}$  long in type species.





**Fig. 19.** A–I. *Cucullitylenchus amazonensis* Huang & Raski, 1986. A. Entire female. B. *En face* view of female head. C. Lateral view of female head. D. Oesophagus of female. E and F. Head ends of female and male, respectively. G. Tail end of male. H and I. Reproductive regions of male and female, respectively. J–O. *Sakia* sp. from sugarcane soil in Venezuela. J. Head end of female. K. Oesophagus of female. L and M. Posterior regions of female and male, respectively. N. Vulval region. O. Spiculum and gubernaculum. A–I. After Huang & Raski (1986).

### Type species

*Cucullitylenchus amazonensis* Huang & Raski, 1986

No other species.

**ETYMOLOGY.** *Cucullus* = hood, refers to cowl-shaped cephalic region, and *Tylenchus*.

The type species was collected from Amazon rain forest near the city of Manaus, State of Amazonas, Brazil.

### Genus *Sakia* Khan, 1964

syn. *Basiliophora* Husain & Khan, 1965

(Fig. 19, J–O)

#### Diagnosis

Tylenchinae. Body slender, about 1 mm or less long, straight to arcuate upon relaxation. Cuticle finely striated, sometimes appearing smooth. Lateral fields each with four incisures. Cephalic region continuous, rounded or conoid, smooth; framework hexaradiate, lightly sclerotized; amphid apertures labial, indistinct. Stylet slender, about 10  $\mu\text{m}$  long; conus shorter than shaft; knobs present, often weakly developed. Orifice of dorsal gland close to stylet base. **Median bulb fusiform, non-muscular, non-valvate.** Isthmus elongate-slender. Basal bulb round, pear-shaped or cylindroid, offset from intestine. **Cardia present.** Excretory pore behind nerve ring, **duct often sclerotized.** Vulva a prominent transverse slit, postmedian; lips not modified. Postvulval uterine sac about one body width or less long. Prodelphic; ovary outstretched. Tail elongate-filiform. Prothasmids dorsal to lateral field, postmedian. Bursa adanal. Spicule and gubernaculum typical of the subfamily.

#### Type species

*Sakia typica* Khan, 1964

#### Other species

- Sakia alii* Suryawanshi, 1971
- S. castori* Khan, Mathur, Nand & Prasad, 1968  
syn. *Basiliophora castori* (Khan *et al.*) Hussain, 1972
- S. indica* (Husain & Khan, 1965) Khan, Mathur, Nand & Prasad, 1968  
syn. *Basiliophora indica* Husain & Khan, 1965
- S. jonesi* (Husain & Khan, 1965) Khan, Mathur, Nand & Prasad, 1968  
syn. *Basiliophora jonesi* Husain & Khan, 1965
- S. propora* (Husain & Khan, 1967) Suryawanshi, 1971  
syn. *Basiliophora propora* Husain & Khan, 1967

#### Nomina nuda

- Sakia attenuata* Kapoor, 1983
- S. bella* Kapoor, 1983
- Basiliophora constricta* Kapoor, 1983
- B. delicata* Kapoor, 1983
- B. filicaudata* Kapoor, 1983

#### Remarks

*Sakia* was proposed by S.H. Khan (1964) in an abstract for a species, *Sakia typica*, which was proposed in the same paper and designated its type species. The description of *S. typica* is meagre and lacks illustrations, but is given separately from the generic characters. It should be regarded as species inquirenda. However, the generic characters are sufficiently demarcated and the genus is compared with

*Boleodorus*. Hence *Sakia* can be accepted as a valid genus. Husain (1972) disputed this and proposed *Sakia* as a *genus dubium*. The type species was never described properly but Khan *et al.* (1968) studied it and consequently synonymized *Basiliophora* Husain & Khan, 1965 with *Sakia*.

ETYMOLOGY. Derived from the initials of Syed Ahmad Khan, founder of the Aligarh Muslim University, India.

*Sakia typica* was collected from around roots of *Plumeria* in Shahjahanpur City, Uttar Pradesh, India.

### Genus *Aglenchus* Andr ssy, 1954 (Meyl, 1961)

syn. *Tylenchus* (*Aglenchus* Andr ssy, 1954)

(Fig. 16, J–Q)

#### Diagnosis

Tylenchinae. Body small (0.35–0.77 mm), straight to slightly arcuate. Cuticle coarsely annulated (annules smooth, about 1–2  $\mu\text{m}$  wide at midbody). **Lateral fields each with two prominently raised ridges** (with three incisures); no other longitudinal ridges besides those in lateral fields. Cephalic region without distinct striation. **Labial plate rectangular, bearing pore-like or crescent-like amphid apertures not extending on lateral sides of cephalic region.** Stylet less than 15  $\mu\text{m}$  long, conus about half total length, knobs rounded. Median bulb round to oval, muscular, with conspicuous refractive thickenings; basal bulb elongate-pyriform; cardia discoidal. Deirids near excretory pore. Prothasms dorso-sublateral, postmedian, in females slightly anterior to vulva. **Vulva sunken in body, with larger outer and smaller inner lips and conspicuous lateral membranes**, at 53–69% of body length. **Vagina directed forward**, its walls often swollen. **Postvulval uterine sac absent.** Spermatheca offset, round to oval, usually with sperm. Tail elongate-filiform, longer than vulva–anus distance. Males usually present, with distinct adanal bursa, 11–16  $\mu\text{m}$  long spicules and **elevated-pointed cloacal lips forming a tubus.** **Labial plate and amphids in male are laterally elongated.**

#### Type species

*Aglenchus agricola* (de Man, 1884) Meyl, 1961

syn. *Tylenchus agricola* de Man, 1884

*Anguillulina agricola* (de Man) Goodey, 1932

*Tylenchus filiformis* apud de Man, 1876 et 1880

*Tylenchus filiformis* de Man, 1876 in Goodey, 1932, nec *T. filiformis* B tschli, 1873

*Tylenchus paragricola* Paetzold, 1958

*Aglenchus paragricola* (Paetzold) Meyl, 1961

#### Other species

*Aglenchus ainakamur  Mizukubo, 1989*

*A. andrassyi* Sultan, 1986

*A. dakotensis* Geraert & Raski, 1989

- A. geraerti* Mizukubo, 1989, was a nom. nov. for *A. muktii* apud Geraert & Raski, 1989, nec *A. muktii* Phukan & Sanwal, 1980  
*A. mardanensis* Maqbool, Shahina & Zarina, 1984  
*A. muktii* Phukan & Sanwal, 1980  
*A. siddiqii* Khan, Khan & Bilquees, 1992

### Species inquirendae

- Tylenchus agricola* var. *aquaticus* Micoletzky, 1922  
 syn. *Aglenchus agricola* var. *aquaticus* (Micoletzky, 1922) Ebsary, 1991  
*Aglenchus parvulus* Husain, 1968

ETYMOLOGY. *Ag* from its type species name *agricola*, and *lenchus* from *Tylenchus*.

The type specimens of the type species were collected by de Man at Leiden or Walcheren; his slide no. H205 containing a female (No. 2) was designated as lecto-type by Loof (1961).

### Genus *Coslenchus* Siddiqi, 1978

syn. *Cosaglenchus* Siddiqui & Khan, 1983

*Paktylenchus* Maqbool, 1983

(Figs 8(d)B; 8(e)D; 43, I–N)

### Diagnosis

Tylenchinae. Body small (0.33–0.65 mm), straight to slightly arcuate when relaxed. Body cuticle **coarsely annulated** (annules 1.5–3.6  $\mu\text{m}$  wide at midbody, 117–228 in number between anterior end of body and anus) **and modified into longitudinal ridges** (except on head and tail tip), 10–22 in number, excluding those of lateral fields, at midbody. Lateral fields with two to three ridges being more elevated than other body ridges. Cuticle surface outside lateral fields showing minute squares or rectangles formed by transverse and longitudinal striae or grooves. Cephalic region continuous or only slightly offset, usually striated. Labial plate dumbbell-shaped, more elongate in male than in female, bearing **round, pore-like amphid apertures not extending on lateral sides of cephalic region**. Stylet under 15  $\mu\text{m}$  long with conus less than half its total length. Median oesophageal bulb pyriform or more elongate; cardia rounded to discoidal. Deirids at level of excretory pore or just posterior to it. Prothasms dorso-sublateral, postmedian, in females usually just behind level of vulva. **Vulva with thick lips and lateral membranes**. Vagina at right angles to body axis or slightly directed forward, with walls appearing swollen. Ovary single, outstretched. Spermatheca usually without sperm. Postvulval uterine sac present, rarely absent. Tail straight, elongate-conoid to filiform. Male usually rare, with adanal bursa and **cloacal lips forming a short tube**.

### Type species

- Coslenchus costatus* (de Man, 1921) Siddiqi, 1978  
 syn. *Tylenchus costatus* de Man, 1921  
*Tylenchus* (*Aglenchus*) *costatus* de Man (Andrássy, 1954)  
*Aglenchus costatus* (de Man) Meyl, 1961

*Anguillulina costata* (de Man) Goodey, 1932  
*Tylenchus buffalorae* Altherr, 1950  
*Anguillulina buffalorae* (Altherr) Altherr, 1952  
*Coslenchus buffalorae* (Altherr) Siddiqi, 1986  
*Tylenchus* (*Aglenchus*) *neozelandicus* Egunjobi, 1967  
*Coslenchus neozelandicus* (Egunjobi) Siddiqi, 1986

#### Other species

*Coslenchus acceptus* Andrásy, 1982 (syn. of *C. costatus* for Geraert & Raski, 1989)  
*C. alacinatus* Siddiqi, 1981  
     syn. *C. brevis* Siddiqui & Khan, 1983  
     *C. lycus* Siddiqui & Khan, 1983  
     *C. tausifi* Siddiqui & Khan, 1983  
*C. andrassyi* Brzeski, 1987  
*C. aquaticus* Geraert & Raski, 1989  
*C. areolatus* (Egunjobi, 1967) Siddiqi, 1978  
     syn. *Tylenchus* (*Aglenchus*) *areolatus* Egunjobi, 1967  
*C. assamensis* (Phukan & Sanwal, 1980) Andrásy, 1982 (syn. of *C. areolatus* for Brzeski, 1998)  
     syn. *Aglenchus assamensis* Phukan & Sanwal, 1980  
     *C. assamensis* (Phukan & Sanwal) Kapoor, 1983  
*C. bilineatus* Sumenkova, 1989  
*C. bisexualis* Siddiqi, 1981  
*C. cancellatus* (Cobb, 1925) Siddiqi, 1978  
     syn. *Tylenchus cancellatus* Cobb, 1925  
     *Anguillulina cancellata* (Cobb) Goodey, 1932  
*C. capsici* Khurma & Gupta, 1988  
*C. cocophilus* Andrásy, 1982  
*C. diversus* Lal & Khan, 1988  
*C. emelcius* Siddiqui & Khan, 1983 (syn. of *C. areolatus* for Brzeski, 1998)  
*C. erectus* Lal & Khan, 1988  
*C. franklinae* Siddiqi, 1981 (syn. of *C. areolatus* for Brzeski, 1998)  
*C. gracilis* Andrásy, 1982  
*C. indicus* (Khan, Chawla & Prasad, 1969) Siddiqi, 1978 (syn. of *C. areolatus* for Brzeski, 1998)  
     syn. *Tylenchus* (*Aglenchus*) *indicus* Khan, Chawla & Prasad, 1969  
*C. japonicus* Mizukubo & Minagawa, 1984  
*C. lateralis* Andrásy, 1982  
*C. leiocephalus* Brzeski, 1998  
*C. lycopersicus* (Husain & Khan, 1976) Siddiqi, 1978  
     syn. *Aglenchus lycopersicus* Husain & Khan, 1976  
*C. maritus* Andrásy, 1991  
*C. modicus* (Siddiqui & Khan, 1983) Siddiqi, 1986  
     syn. *Cosaglenchus modicus* Siddiqui & Khan, 1983  
     *C. modicus* (Siddiqui & Khan) Mizukubo & Minagawa, 1986  
*C. multigyrus* Siddiqi, 1981  
*C. oligogyrus* Brzeski, 1987

- syn. *Coslenchus oligoridjus* Sumenkova, 1989 (syn. by Brzeski, 1998)
- C. pastor* Andr  ssy, 1982
- C. polonicus* Brzeski, 1982
- C. polygyrus* Bajaj & Bhatti, 1983
- C. pycnocephalus* Siddiqui, 1981
- C. rafiqi* (Siddiqui & Khan, 1983) Siddiqui, 1986  
syn. *Cosaglenchus rafiqi* Siddiqui & Khan, 1983 (was named after M. Rafiq Siddiqui, original spelling *rafikus*)  
*Coslenchus rafiqi* (Siddiqui & Khan, 1983) Mizukubo & Minagawa, 1986
- C. rhombus* Andr  ssy, 1982 (syn. of *C. alacinatus* for Ebsary, 1991)
- C. rugosus* Andr  ssy, 1982
- C. siddiqui* Andr  ssy, 1982
- C. temperatus* Siddiqui & Khan, 1983 (syn. of *C. cocophilus* for Geraert & Raski, 1989)
- C. tuberosus* (Maqbool, 1983) Siddiqui, 1986  
syn. *Paktylenchus tuberosus* Maqbool, 1983  
*C. tuberosus* (Maqbool) Mizukubo & Minagawa, 1986
- C. turkeyensis* Siddiqui, 1981

#### Nomen nudum

*Coslenchus temperatus* Kapoor, 1983

#### Notes

Mizukubo & Minagawa (1986) discussed the phylogenetic relationships and proposed the synonymy of *Cosaglenchus* and *Paktylenchus* with *Coslenchus* in the December (1985) issue of volume 15 of the Japanese Journal of Nematology, published on 24 March, 1986 (personal communication with Dr Mizukubo). Siddiqui (January, 1986) had also proposed this synonymy.

ETYMOLOGY. From its type species name *costatus*, and *lenchus* from *Aglenchus*.

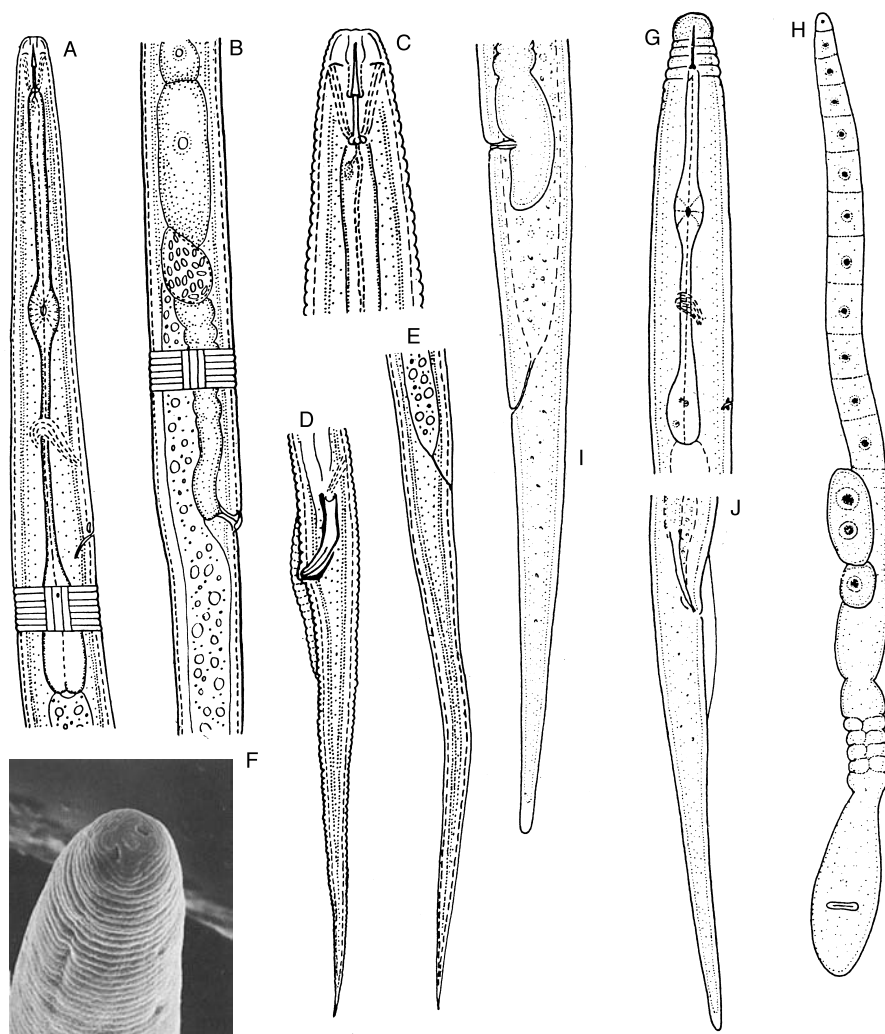
The type habitat and locality for the type species is moist soil under plants on the bank of the River Mark in a suburb of Breda, Holland. Keys to *Coslenchus* spp. have been given by Andr  ssy (1982) and Geraert & Raski (1989).

#### Genus *Fraglenchus* gen. n.

(Fig. 20, A–F)

#### Diagnosis

Tylenchinae. Body small (0.33–0.57 mm), straight when relaxed. Cuticle finely but not deeply annulated; annules smooth. **Lateral fields each with two prominently raised ridges separated by a third narrow ridge** (i.e. with four incisures); no other longitudinal ridges besides those in lateral fields. Cephalic region rounded, distinctly and finely striated. **Labial plate four-lobed, with six labial papillae around oral aperture. Amphid apertures small oblique slits near but outside lateral margins of labial plate, not extending on lateral sides of cephalic region.** Stylet less than 10 µm long, conus shorter than half total length, knobs small, rounded. Dorsal



**Fig. 20.** A–F. *Fraglenchus fragariae* (Szczygiel) gen. n., comb. n. G–J. *Cervoannulatus graminus* Bajaj, 1998. A and G. Oesophageal regions of female. B and H. Reproductive regions of females. C. Head end of female. D and J. Tail ends of male. E. Tail end of female. F. Scanning electron micrograph of anterior end showing amphidial aperture. I. Posterior region of female. (A–E. After Szczygiel (1969). F. After Geraert and Raski (1989). G–J. After Bajaj (1998).)

gland opening just behind stylet base. Median bulb oval, muscular, with conspicuous refractive thickenings; basal bulb elongate-pyriform; cardia rounded. Deirids a little behind excretory pore. **Vulva in a body cavity four to five annules wide, with conspicuous lateral membranes, at 64–69% of body length. Vagina directed forward, its walls not swollen. Postvulval uterine sac absent.** Tail elongate-conoid. Males

with adanal bursa, spicules arcuate, 11–12  $\mu\text{m}$  long in type species, gubernaculum trough-shaped and **cloacal lips rounded, not forming a tubus**.

#### Type species

*Fraglenchus fragariae* (Szczygieł, 1969) comb. n.

syn. *Aglenchus fragariae* Szczygieł, 1969

*Filenchus fragariae* (Szczygieł) Geraert & Raski, 1988

No other species.

#### Relationship

*Fraglenchus* gen. n. comes close to *Aglenchus* Andrassy in having amphidial apertures confined to the front of the head, large lateral vulval membranes and no postvulval uterine sac, but differs from it in having finely striated cuticle on head and body, four incisures in lateral field, amphidial apertures outside labial plate (Fig. 20, F), vaginal wall not swollen and male cloacal lips not tube-like. It differs from *Zanenchus* Siddiqi in having cuticle not deeply annulated, four incisures in lateral field, large lateral vulval membranes and cloacal lips not tube-like. It differs from *Filenchus* in having amphidial apertures not being longitudinally straight slits and extending on lateral sides of cephalic region and in lacking a postvulval uterine sac. For a description of *Fraglenchus fragariae*, the type species, see Szczygieł (1969), Andrassy (1980) and Geraert & Raski (1989).

ETYMOLOGY. *Fr* from type species name *fragariae*, and *Aglenchus*.

*Fraglenchus fragariae* was found in sandy soil around roots of strawberry (*Fragaria* sp.), at Plebanka, Gostynin district, Poland.

#### Genus *Cervoannulatus* Bajaj, 1998

(Fig. 20, G–J)

#### Diagnosis

Tylenchinae. Body under 0.5 mm long, slightly arcuate upon relaxation. **Cuticle smooth except near head where it is coarsely annulated. Lateral field indistinct.** Cephalic region high, inflated being rounded and offset, not striated; framework lightly sclerotized. Amphidial apertures indistinct. Deirids and prothasms not reported. Stylet small, 8  $\mu\text{m}$  long in type species; **conus about as long as shaft**; basal knobs small, rounded. Orifice of dorsal gland 3  $\mu\text{m}$  behind stylet base in type species. **Median bulb oval, muscular, with refractive thickenings**, just anterior to mid-oesophagus. Isthmus elongate-slender. Basal bulb small, pyriform, offset from intestine. **Cardia discoidal**. Excretory pore well behind nerve ring, opposite basal bulb in type species. Vulva a prominent transverse slit, in posterior region at 43–54  $\mu\text{m}$  from anus in type species; lips not modified. Vagina perpendicular to body axis. Ovary outstretched, oocytes in a single file. Spermatheca bilobed, offset. **Crustaformeria quadricolumellate**. Postvulval uterine sac distinct, less than one body width long. Tails elongate-tapering ( $c' = 7\text{--}8$ ) to a bluntly rounded terminus. Bursa adanal, covering about one-fifth of tail. Spicules cephalated, almost straight, thin, 16  $\mu\text{m}$  long in type species. Gubernaculum small, trough-shaped.



## Type species

*Cervoannulatus graminus* Bajaj, 1998

No other species.

ETYMOLOGY. Generic name means annulated neck, refers to cuticle annulated only in the anteriormost part of the neck region.

The type species was collected from around roots of *Desmostachya bipinnata* Stapf. growing wild near Kirara village in Hisar district, Haryana State, India.

**Genus *Polenchus* Andr ssy, 1980**

(Fig. 21, A–G)

## Diagnosis

Tylenchinae. Body medium sized (about 0.6 mm), straight to arcuate. **Cuticle smooth, devoid of transverse or longitudinal striation. Lateral fields inconspicuous, not raised above body surface.** Lip region continuous, rounded. Amphidial apertures longitudinal, ventrally curved slits. Stylet 14–15  $\mu\text{m}$  long in type species; conus about half its length; knobs large, more or less triangular. Median bulb oval, muscular, with refractive thickening. Basal bulb saccate. Deirids a little behind excretory pore. Vulva submedian, transverse, lips not raised, without lateral membranes. Vagina thick-walled, almost at right angles to body axis. An elongate-oval, offset, anteriorly directed spermatheca and a postvulval uterine sac present. Bursa small, low, in lateral view not projecting beyond body contour.

## Type species

*Polenchus politus* Andr ssy, 1980

## Other species

*Polenchus curvicauda* Raski & Geraert, 1988

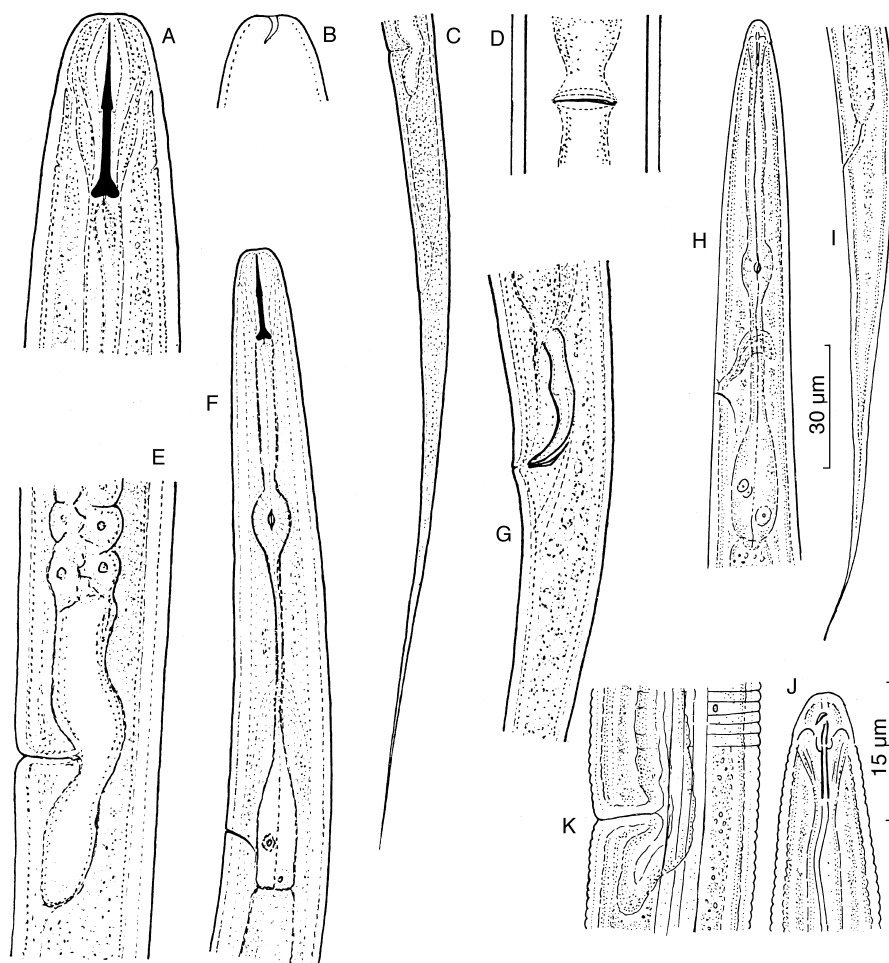
*P. shamimi* Baqri, 1991

## Note

*Polenchus curvicauda* Raski & Geraert, 1988 has thick cuticle with faint annulation, unobservable lateral field, amphidial aperture as longitudinal slit and a weakly developed, adanal bursa. The differentiation of *Polenchus* from *Filenchus* has now become difficult.

ETYMOLOGY: *Pol* from type species name *politus*, and Greek *enchos* = spear.

*Polenchus politus* was found in wet moss from a rock at Mt Kaindi, New Guinea.



**Fig. 21.** A–G. *Polenchus politus* Andrassy. H–K. *Neopsilenchus magnidens* (Thorne) from Yugoslavia. A and J. Head ends of female. B. Amphidial aperture. C and I. Tail ends of female. D. Vulva in ventral view. E and K. Vulval regions (note prothasmid in K). F and H. Oesophageal regions of female. G. Spicular region. (A–G. After Andrassy, 1980.)

### Subfamily Boleodorinae Khan, 1964 syn. Basiriinae Decker, 1972

#### Diagnosis

Tylenchidae. About 1 mm or less long. Cuticle finely striated. Lateral fields each with four incisures (inner incisures indistinct in some spp.). Deirids present. Prothasms generally obscure. Cephalic region conoid-rounded, generally elevated and smooth. Amphidial apertures prominent, oblique or longitudinal slits or

**inverted V-shaped, partially covered by a cuticular flap, postlabial**, just behind level of cephalic papillae. Stylet delicate, conus shorter than shaft, knobs weakly developed, round, flanged or absent (*Neopsilenchus*). **Orifice of dorsal oesophageal gland generally at a quarter or more of stylet length behind stylet base.** Postcorpus muscular or non-muscular, with or without refractive thickenings. Basal bulb offset from intestine. Vulval lips not modified, lateral membranes absent. Postvulval uterine sac present. Spermatheca lobed, usually offset. Ovary and testis outstretched. Sperm small sized. Spicules and gubernaculum typical of the family. Cloacal lips not tube-like. Bursa adanal, simple. Tails generally filiform, may be elongate-conoid, terminus finely pointed, rounded, clavate or notched.

#### Type genus

*Boleodorus* Thorne, 1941

#### Other genera

*Basiria* Siddiqi, 1959

*Neopsilenchus* Thorne & Malek, 1968

#### Key to genera of Boleodorinae

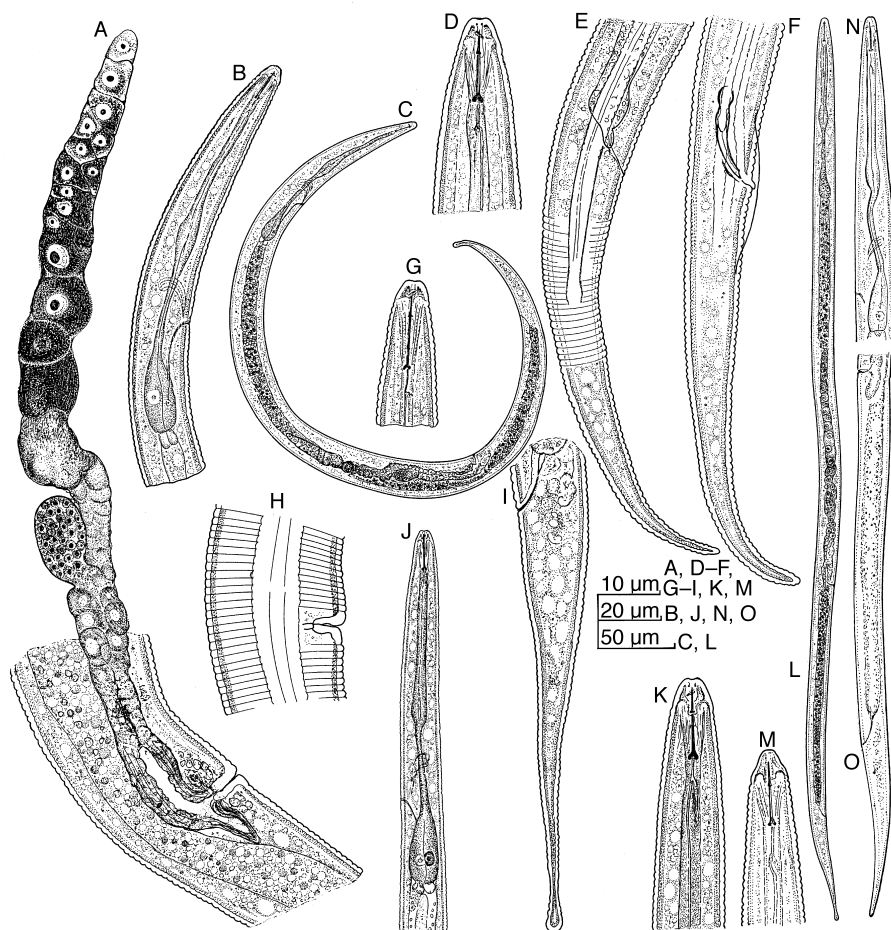
1. Body usually C-shaped; stylet base flanged; median oesophageal bulb without cuticular thickening ..... *Boleodorus*  
 Body straight to slightly arcuate; stylet base plain or with minute knobs; median oesophageal bulb mostly with cuticular thickening ..... 2
2. Stylet with basal knobs ..... *Basiria*  
 Stylet without basal knobs ..... *Neopsilenchus*

#### Genus *Boleodorus* Thorne, 1941

(Figs 8(e)A; 22, A–H)

#### Diagnosis

Boleodorinae. Body under 1 mm (0.33–0.72 mm), **ventrally arcuate to more curved, C-shaped**. Cuticle finely annulated. Lateral field with four incisures, not areolated. Cephalic region elevated, conoid-rounded, smooth, with or without a depression at oral aperture; framework weakly to moderately sclerotized. Amphid apertures oval or crescent-like slits, obliquely placed on the head. Stylet generally 8–10 µm long; conus about one-third of total stylet length; **knobs flanged**. Dorsal oesophageal gland 1–4 µm from stylet base. **Corpus cylindroid, with a basal fusiform swelling devoid of musculature and inner refractive thickenings; distance from anterior end to its base generally greater than that from latter to oesophageal base.** Basal bulb pyriform. Excretory pore behind nerve ring; terminal excretory duct generally sclerotized. Vulva generally at 59–75% of body length. Postvulval uterine sac short, less than a body width. Spermatheca offset, oval or elongate. **Ovary short, with oocytes in one or multiple rows. Tail elongate-conoid, ventrally arcuate. Bursa adanal.** Spicules and gubernaculum typical of the family.



**Fig. 22.** A–H. *Boleodorus thylactus* Thorne, from grass soil at Luton, England. I–L. *Basiria clavicaudata* (Thorne) from sugarcane soil in Venezuela. M–O. *Basiria citri* (Javed) paratype female. A. Vulval region and gonoduct. B, J and N. Oesophageal regions. C and L. Females. D, K and M. Head ends of females. E and I. Tail ends of females. F. Tail end of male. G. Head end of male. H. Vulval region. O. Posterior region of female.

#### Type species

*Boleodorus thylactus* Thorne, 1941

#### Other species

*Boleodorus abnormus* Khan & Basir, 1964

*B. acurvus* Jairajpuri, 1982

*B. azadkashmirensis* Maqbool, Shahina & Firoza, 1990

*B. acutus* Thorne & Malek, 1968 (nec *B. acutus* Husain & Khan, 1974 = *B. filiformis* Husain & Khan, 1977)

- B. citri* Edward & Rai, 1970  
*B. constrictus* Rahman & Ahmad, 1996  
*B. cylindricus* Dhanachand, Renubala & Anandi, 1993  
*B. cynodoni* Fotedar & Mahajan, 1974  
*B. filiformis* Husain & Khan, 1977  
     syn. *B. acutus* Husain & Khan, 1974 (= primary homonym of *B. acutus* Thorne & Malek, 1968)  
*B. flexuosus* Eroshenko, 1982  
*B. hyderi* Husain & Khan, 1965  
*B. impar* Khan & Basir, 1964  
*B. innuptus* (Andrássy, 1961) Siddiqi, 1963  
     syn. *Nothotylenchus innuptus* Andrássy, 1961  
         *Ditylenchus innuptus* (Andrássy) Fortuner & Maggenti, 1987  
*B. mirus* Khan, 1964  
*B. modicus* Lal & Khan, 1988  
*B. neosimilis* Geraert, 1971  
     syn. *B. similis* Thorne & Malek, 1968 (= primary homonym of *B. similis* Khan & Basir, 1963)  
*B. pakistanensis* Siddiqi, 1963  
*B. punici* Gambhir & Dhanachand, 1997  
     syn. *Boleodorus* (*Neobasiria*) *punici* Gambhir & Dhanachand, 1997  
*B. rafiqi* Husain & Khan, 1965 (syn. of *B. thylactus* for Khera, 1970)  
*B. similis* Khan & Basir, 1963 (nec *B. similis* Thorne & Malek, 1968 (= *B. neosimilis* Geraert, 1971))  
     syn. *B. arachis* Maqbool & Ghazala, 1986, syn. n.  
*B. spiralis* Egunjobi, 1968  
*B. tenuis* Lal & Khan, 1988  
*B. teres* Nanjappa & Khan, 1972  
*B. volutus* Lima & Siddiqi, 1963  
*B. zaini* Maqbool, 1982

## Notes

Siddiqi (1986) recognized two subgenera under *Boleodorus*, viz. *Boleodorus* (*Boleodorus*) and *B. (Neobasiria)*. *Neobasiria* is considered here as a synonym of *Basiria* and is not recognized as a subgenus of *Boleodorus*. *Boleodorus atypicus* Khera & Chaturvedi, 1977, *B. longistylus* Khera & Chaturvedi, 1977 and *B. typicus* Husain & Khan, 1968 were transferred to the genus *Nothotylenchus* by Siddiqi (1986).

Mathur *et al.* (1966) proposed the genus *Boleodoroides*, with *B. oryzae* Mathur, Khan & Prasad, 1966 as its type species. Geraert (1971) studied a paratype female of *B. oryzae* and noticed the *Ditylenchus*-type head, indistinct amphids, lateral field with six incisures, elongated postvulval uterine sac, presence of a crustaformeria (quadricolumella) and oesophageal base resembling that of *Paurodontus* and, hence, transferred the genus *Boleodoroides* to the subfamily Paurodontinae. Siddiqi (1986) examined paratypes of *B. oryzae* at the Indian Agricultural Research Institute, New Delhi, and found the species to belong to the genus *Nothotylenchus*, to which it was transferred as *Nothotylenchus oryzae* (Mathur, Khan & Prasad, 1966) Siddiqi, 1986 and *Boleodoroides* was synonymized with *Nothotylenchus*.

ETYMOLOGY. Greek *bolys*, *boleos* = harpoon, and *dory* = spear.

The type species was found in cultivated soil in Utah, USA.

### Genus *Basiria* Siddiqi, 1959

syn. *Tylenchus* (*Clavilenchus* Jairajpuri, 1966)

*Clavilenchus* Jairajpuri, 1966

*Basiroides* Thorne & Malek, 1968 (Thorne & Malek, 1968)

*Neobasiria* Javed, 1982

*Duotylenchus* Saha & Khan, 1982

*Pseudobasiria* Jahan, 1986

*Basirienchus* Geraert & Raski, 1986; syn. n.

*Rhabdotylenchus* Hui, Zhixin, Shaomei & Youqin, 1994; syn. n.

(Figs 22, I–L; 23)

### Diagnosis

Boleodorinae. Body about 1 mm or less long, straight to arcuate ventrally upon relaxation. Cuticle thin, with distinct fine annules. Lateral fields each with four incisures, rarely inner incisures indistinct (e.g. *B. gracilis*). **Amphidial apertures prominent, slit-like**, or inverted V-shaped, **located at base of lateral lip areas**, posterior to cephalic sensilla. Prothasms indistinct, dorso-sublateral, outside lateral fields, 0.5–1 body width anterior to vulva in type species. Cephalic region elevated, rounded, smooth; framework lightly sclerotized, with outer margins extending well into body; lateral lip areas generally smaller than submedians. Stylet slender, about 9–13  $\mu\text{m}$  long, with small **rounded knobs**. Orifice of dorsal oesophageal gland **up to one stylet length behind stylet base**. Median bulb generally poorly developed, with or without refractive thickenings, at 36–58% of oesophageal length. Basal bulb offset from intestine, with distinct lumen. Cardia distinct. Vulva at about 60–70% of body length. Spermatheca usually lobed. Ovary single, outstretched. Postvulval uterine sac present, shorter than body width. Tail elongate-filiform, with clavate, rounded, indented or pointed terminus. Bursa adanal. Spicules 14–24  $\mu\text{m}$  long; gubernaculum simple, fixed.

### Type species

*Basiria graminophila* Siddiqi, 1959

syn. *Tylenchus* (*Filenchus*) *graminophilus* (Siddiqi) Goodey, 1963

*B. asaraensis* Khan, 1982 (syn. by Karegar & Geraert, 1997c)

*B. bajorensis* Khan & Bilquees, 1994

*B. incita* Szczygieł, 1970

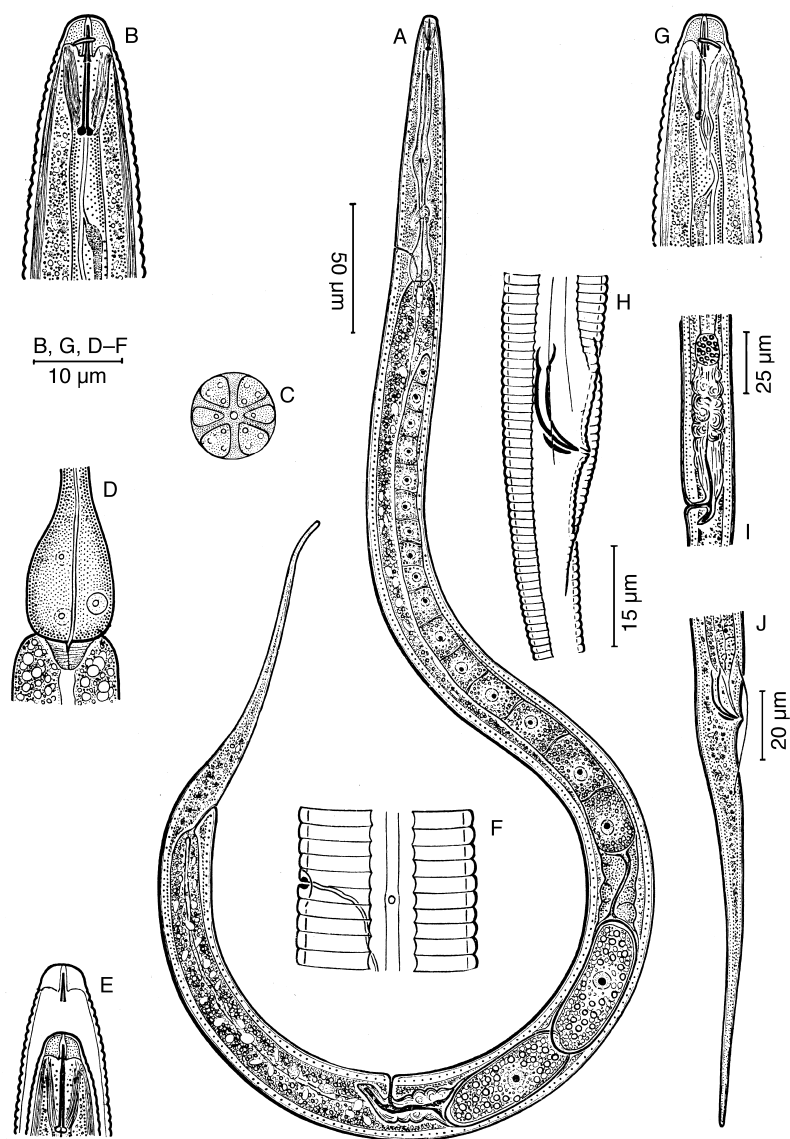
*B. nasikensis* Darekar & Khan, 1979

*B. pakhi* Hashim, 1985 (was a nom. nov.)

syn. *Basiria elegans* Patil & Khan, 1983, nec *Basiria elegans* (Khan & Khan, 1975)

Bajaj & Bhatti, 1979

*B. patili* Fortuner, 1985 (= objective syn. of *B. elegans* Patil & Khan, 1983)



**Fig. 23.** *Basiria graminophila* Siddiqi. A. Female. B and G. Anterior end of female and male, respectively. C. Cross-section of head. D. Basal oesophageal bulb and cardia. E. Anterior end of moulting juvenile. F. Deirid and excretory pore. H. Spicular region. I. Vulval region. J. Tail end of male. (After Siddiqi (1959), courtesy *Nematologica*.)

#### Other species

*Basiria aberrans* (Thorne, 1949) Siddiqi, 1963

syn. *Psilenchus aberrans* Thorne, 1949

*Tylenchus (Filenchus) neoaberrans* Goodey, 1963 (nec *Tylenchus aberrans* (Altherr, 1952) Andr  ssy, 1954 (= *Filenchus altherri*))

- B. affinis* Thorne & Malek, 1968
- B. babhi* Siddiqi, 1986 (was a nom. nov.)  
syn. *Basiria indica* Bajaj & Bhatti, 1979 (= junior secondary homonym of *B. indica* (Chawla *et al.*, 1968))
- B. berylla* (Khan & Khan, 1975) Bajaj & Bhatti, 1979  
syn. *Basiroides beryllus* Khan & Khan, 1975  
*Basiroides citri* Maqbool, Fatima & Shahina, 1984  
*Basiria citri* (Maqbool, Fatima & Shahina) Siddiqi, 1986  
*Basiria neocitri* (Maqbool, Fatima & Shahina, 1984) Ebsary, 1991 (was nom. nov. for *Basiria citri* (Maqbool, Fatima & Shahina) Siddiqi, 1986, nec. *B. citri* (Javed, 1982) Hashim, 1985)
- B. bilineata* (Saha & Khan, 1982) Ebsary, 1991  
syn. *Duotylenchus bilineatus* Saha & Khan, 1982
- B. binaria* (Sultana, 1980) Hashim, 1985  
syn. *Basiroides binarius* Sultana, 1980
- B. brevia* (Sultana, 1980) Hashim, 1985  
syn. *Basiroides brevius* Sultana, 1980
- B. brevistylus* (Khera, 1970) Ebsary, 1991  
syn. *Boleodorus* (*Boleodoroides*) *brevistylus* Khera, 1970  
*Boleodorus* (*Neobasiria*) *brevistylus* Khera, 1970 (Siddiqi, 1986)
- B. citri* (Javed, 1982) Hashim, 1985  
syn. *Neobasiria citri* Javed, 1982  
*Boleodorus* (*Neobasiria*) *citri* (Javed) Siddiqi, 1986
- B. clavicaudata* (Thorne, 1941) Ebsary, 1991  
syn. *Boleodorus clavicaudatus* Thorne, 1941  
*Boleodoroides clavicaudatus* (Thorne) Mathur, Khan & Prasad, 1966  
*Boleodorus* (*Neobasiria*) *clavicaudatus* Thorne, 1941 (Siddiqi, 1986)
- B. diversicauda* F.A. Khan, 1993
- B. dolichurus* Loof, 1971  
syn. *Basiroides dolichurus* (Loof) Maqbool, Fatima & Shahina, 1984
- B. duplexa* (Hagemeyer & Allen, 1952) Geraert, 1968  
syn. *Psilenchus duplexus* Hagemeyer & Allen, 1952  
*Tylenchus* (*Filenchus*) *duplexus* (Hagemeyer & Allen) Andr  ssy, 1954  
*Filenchus duplexus* (Hagemeyer & Allen) Meyl, 1961 (Baker, 1962 also proposed this combination)  
*Basiroides duplexus* (Hagemeyer & Allen) Khan, 1973 (Maqbool *et al.*, 1984, also proposed this combination)  
*Basiroides conurus* Thorne & Malek, 1968 (syn. by Karegar & Geraert, 1997b)  
*Basiria conurus* (Thorne & Malek, 1968) Fotedar & Mahajan, 1973  
*Basiroides obliquus* Thorne & Malek, 1968 (syn. by Karegar & Geraert, 1997b)  
*Basiria obliqua* (Thorne & Malek) Fotedar & Mahajan, 1973
- B. elegans* (Khan & Khan, 1975) Bajaj & Bhatti, 1979  
syn. *Basiroides elegans* Khan & Khan, 1975
- B. flandriensis* Geraert, 1968  
syn. *Basiroides flandriensis* (Geraert) Khan, 1973 (Maqbool *et al.*, 1984, also proposed this combination)



- B. gracilis* (Thorne, 1949) Siddiqi, 1963  
 syn. *Psilenchus gracilis* Thorne, 1949  
*Tylenchus* (*Filenchus*) *neogracilis* Goodey, 1963 (was a nom. nov.)  
*Acusilenchus bilineatus* Shahina & Maqbool, 1990  
*Basiria bilineata* (Shahina & Maqbool, 1990) Karegar & Geraert, 1997 (syn. by Karegar & Geraert, 1997a; secondary homonym of *B. bilineata* (Saha & Khan, 1982))  
*Neopsilenchus* (*Acusilenchus*) *bilineatus* Shahina & Maqbool, 1990
- B. guangdongensis* (Hui, Zhixin, Shaomei & Youqin, 1994) comb. n.  
 syn. *Rhabdotylenchus guangdongensis* Hui, Zhixin, Shaomei & Youqin, 1994
- B. haki* Fotedar & Mahajan, 1973
- B. hiberna* Bernard, 1980
- B. hissariensis* Bajaj & Bhatti, 1979  
 syn. *Basiroides hissariensis* (Bajaj & Bhatti) Maqbool, Fatima & Shahina, 1984
- B. imphalensis* Renubala & Dhanachand, 1992
- B. indica* (Chawla, Bhamburkar, Khan & Prasad, 1968) Khan & Nanjappa, 1971  
 syn. *Trophurus indicus* Chawla, Bhamburkar, Khan & Prasad, 1968
- B. jirians* Renubala & Dhanachand, 1992
- B. kashmirensis* Jairajpuri, 1965  
 syn. *Tylenchus* (*Filenchus*) *kashmirensis* (Jairajpuri) Jairajpuri, 1966
- B. lathyrae* Kakar, Siddiqui & Khan, 1994
- B. lauta* Randhawa, Khera & Khan, 1996
- B. macrostriata* (Sultana, 1980) Hashim, 1985  
 syn. *Basiroides macrostriatus* Sultana, 1980
- B. obscura* Szczygieł, 1970
- B. paraobliqua* (Kazachenko, 1975) Bajaj & Bhatti, 1979 (syn. of *Filenchus vulgaris* for Brzeski, 1997)  
 syn. *Basiroides paraobliquus* Kazachenko, 1975
- B. pravamphidia* Andrásy, 1963  
 syn. *Tylenchus* (*Filenchus*) *pravamphidius* (Andrásy) Jairajpuri, 1966
- B. ritteri* (Baqri & Jairajpuri, 1969) Bernard, 1980  
 syn. *Tylenchus* (*Clavilenchus*) *ritteri* Baqri & Jairajpuri, 1969  
*Clavilenchus ritteri* (Baqri & Jairajpuri) Baqri & Jairajpuri, 1969  
*Basiroides sindhicus* Maqbool, Fatima & Shahina, 1984  
*Basiria sindhica* (Maqbool et al.) Siddiqi, 1986  
*Pseudobasiria sindhica* (Maqbool et al.) Jahan, 1986
- B. shahidi* Khan, 1982
- B. siddiqii* (Sultana, 1980) Hashim, 1985  
 syn. *Basiroides siddiqii* Sultana, 1980
- B. simhai* Das & Sultana, 1980
- B. similis* (Thorne & Malek, 1968) Bernard, 1980  
 syn. *Clavilenchus similis* Thorne & Malek, 1968  
*Basiroides similis* (Thorne & Malek) Maqbool, Fatima & Shahina, 1984
- B. solomonensis* (Ye & Geraert, 1997) comb. n.  
 syn. *Boleodorus solomonensis* Ye & Geraert, 1997  
*Boleodorus* (*Neobasiria*) *solomonensis* Ye & Geraert, 1997
- B. tanuis* Randhawa, Khera & Khan, 1996

- B. tritici* Fotedar & Mahajan, 1973  
*B. tumida* (Colbran, 1960) Geraert, 1968  
 syn. *Psilenchus tumidus* Colbran, 1960  
*Tylenchus* (*Clavilenchus*) *tumidus* (Colbran) Jairajpuri, 1966  
*Clavilenchus tumidus* (Colbran) Thorne & Malek, 1968  
*Basiroides tumidus* (Colbran) Maqbool, Fatima & Shahina, 1984  
*Basiria paratumida* Sakwe & Geraert, 1994 (syn. by Karegar & Geraert, 1997b)  
*B. uncinata* (Geraert & Raski, 1986) comb. n.  
 syn. *Basirienchus uncinatus* Geraert & Raski, 1986  
*B. varians* (Khan & Khan, 1976) Bajaj & Bhatti, 1979  
 syn. *Neopsilenchus varians* Khan & Khan, 1976  
*N.* (*Acusilenchus*) *variens* (Khan & Khan) Shahina & Maqbool, 1990  
*Acusilenchus varians* (Khan & Khan) Shahina & Maqbool, 1990

#### Nomina nuda

- Basiria abrupta* Kapoor, 1983  
*B. leptolongimatrix* (Kazachenko, 1975) Bajaj & Bhatti, 1979  
 syn. *Basiroides leptolongimatrix* Kazachenko, 1975  
 (Note: *leptolongimatrix* is an inadvertent error in spelling of *longimatrix* in Bajaj & Bhatti, 1979. *Basiroides longimatrix* Kazachenko, 1975 is now *Ditylenchus longimatrix* (Kazachenko) Brzeski, 1983.)  
*B. simulata* Kapoor, 1983

#### Remarks

*Basiria* was erected by Siddiqi (1959) and synonymized with *Tylenchus* (*Filenchus*) by Goodey (1963). It was rediagnosed and reinstated by Siddiqi (1963a). Jairajpuri (1966) followed Goodey (1963) in not recognizing *Basiria* as a valid genus, but he proposed a new subgenus, *Clavilenchus*, for *Psilenchus tumidus* Colbran, 1960, on the basis of the tail having a clavate terminus. Geraert (1968) reviewed the genus *Basiria* and transferred *Psilenchus tumidus* to *Basiria*, synonymizing *Clavilenchus* with it.

*Basiroides* was erected by Thorne & Malek (1968) for *Basiria*-like species having a median oesophageal bulb located anterior to the middle of the oesophagus. It was not recognized by Fotedar & Mahajan (1973) but was synonymized with *Basiria* by Bajaj & Bhatti (1979). *Neobasiria* Javed, 1982 was proposed as a junior synonym of *Basiria* by Hashim (1985). *Basiroides nortoni* Elmiligy, 1971 is now *Ditylenchus nortoni* (Elmiligy) Bello & Geraert, 1972.

Geraert & Raski (1986) proposed the genus *Basirienchus* with *B. uncinatus* Geraert & Raski, 1986 as the type species. In this genus they also included two new species, described as *B. costatus* and *B. elenae*. These species have longitudinal cuticular ridges besides the lateral fields and are here assigned to two different genera – *B. costatus* to *Neothada* as *N. costata* and *B. elenae* to a new genus, *Ridgellus*, as *Ridgellus elenae*, its type species.

Karegar & Geraert (1997b) synonymized *Basiria conura* and *B. obliqua* with *B. duplex*, *B. citri* with *B. berylla*, and *B. paratumicauda* with *B. tumicauda*. Karegar & Geraert (1997c) synonymized *B. asaraensis*, *B. bajorensis*, *B. incita*, *B. nasikensis* and *B. pakhi* with *B. graminophila*.

ETYMOLOGY. Patronym honouring Professor Mohammed Abdul Basir (Aligarh Muslim University), who initiated me into nematology. My first proposed new genus.

The type species was found around the roots of grass, *Cynodon dactylon* Pers. and also of citrus at Aligarh, India. *Basiria ritteri* was recorded for China and Vietnam, *B. aberrans* for China and *B. berylla* for Iran (Karegar & Geraert, 1997b,c). A list of and a key to the species of *Basiria* are provided by Karegar & Geraert (1998).

**Genus *Neopsilenchus* Thorne & Malek, 1968**  
**syn. *Acusilenchus* Shahina & Maqbool, 1990**  
 (Figs 8(e)B; 21, H–K)

**Diagnosis**

Boleodorinae. Body under 1 mm (0.4–0.9 mm), ventrally arcuate upon relaxation. Lateral fields each with four incisures. Amphidial apertures slit-like, transverse or oblique. Cephalic region elevated, rounded or conoid-rounded. Stylet cylindroid, 8–15  $\mu\text{m}$ , conus asymmetrical, lumen distinct or solid-appearing anteriorly; **basal knobs absent**; orifice of dorsal gland close to stylet base. Median bulb muscular, with refractive thickenings, near middle of oesophagus. Cardia distinct. Vulva at 60–65% of body length. Ovary single, outstretched. Postvulval uterine sac shorter than body width, with distinct lumen. Tail elongate-filiform, with pointed or rounded tip. Sperm rod-shaped or rounded. Spicules short (11–15  $\mu\text{m}$ ). Gubernaculum simple. Bursa adanal.

**Type species**

- Neopsilenchus magnidens* (Thorne, 1949) Thorne & Malek, 1968  
 syn. *Psilenchus magnidens* Thorne, 1949  
*Tylenchus* (*Filenchus*) *magnidens* (Thorne) Goodey, 1963  
*Basiria magnidens* (Thorne) Geraert, 1968  
*N. (Acusilenchus) curvistylus* Shahina & Maqbool, 1990 (syn. by Karegar & Geraert, 1997)  
*N. peshawarensis* Shahina & Maqbool, 1990 (syn. by Karegar & Geraert, 1997)

**Other species**

- Neopsilenchus affinis* Khan & Khan, 1976  
 syn. *Basiria affinis* (Khan & Khan) Bajaj & Bhatti, 1979  
 nec *Basiria affinis* Thorne & Malek, 1968  
*Basiria loofi* Bajaj & Bhatti, 1979 (was a nom. nov. for *B. affinis* (Khan & Khan, 1976))  
*N. citri* (Jairajpuri, 1968) Bello, 1972  
 syn. *Tylenchus* (*Filenchus*) *citri* Jairajpuri, 1968  
*N. (Acusilenchus) citri* (Jairajpuri) Shahina & Maqbool, 1990  
*Acusilenchus citri* (Jairajpuri) Shahina & Maqbool, 1990  
*N. longicaudatus* Sultan, Singh & Sakhuja, 1988

- syn. *N. (Acusilenchus) longicaudatus* (Sultan *et al.*) Shahina & Maqbool, 1990  
*Acusilenchus longicaudatus* (Sultan *et al.*) Shahina & Maqbool, 1990  
*N. minor* (Geraert, 1968) Kheiri, 1972  
 syn. *Basiria minor* Geraert, 1968  
*N. minutus* Dhanachand, Renubala & Anandi, 1993  
*N. noctiscriptus* (Andrássy, 1962) Khan, 1973  
 syn. *Psilenchus noctiscriptus* Andrássy, 1962  
*Tylenchus (Filenchus) noctiscriptus* (Andrássy) Goodey, 1963  
*Basiria noctiscripta* (Andrássy) Geraert, 1968  
*Tylenchus noctiscriptus* (Andrássy) Brzeski, 1968  
*N. (Acusilenchus) noctiscriptus* (Andrássy) Shahina & Maqbool, 1990  
*Acusilenchus noctiscriptus* (Andrássy) Shahina & Maqbool, 1990  
*N. paragracilis* (Geraert & Raski, 1986) comb. n.  
 syn. *Basiria paragracilis* Geraert & Raski, 1986  
*N. prasadi* Gambhir & Dhanachand, 1997  
*N. similis* Khan & Khan, 1976  
 syn. *Basiria similis* (Khan & Khan) Bajaj & Bhatti, 1979  
*Basiria bajaji* Hashim, 1985, was a nom. nov. for *B. similis* (Khan & Khan)

#### Note

*Basiria paragracilis* Geraert & Raski, 1986 has stylet without basal knobs and elongate spermatheca with relatively large sperm and hence has been transferred to *Neopsilenchus*. A key to *Neopsilenchus* spp. is given by Karegar and Geraert (1997).

ETYMOLOGY. From the Greek *neos* = young, new, and *Psilenchus*.

The type habitat and locality for the type species is an alfalfa field near Hollday, a suburb of Salt Lake City, Utah, USA.

### Subfamily Thadinae Siddiqi, 1986

#### Diagnosis

Tylenchidae. Body under 1 mm long, not extremely slender, straight to arcuate upon relaxation. **Cuticle coarsely annulated; longitudinal striae or grooves may be present.** Lateral fields wide, with four prominent incisures. Prothasms not seen. Amphidial apertures longitudinal slits, near oral opening. Cephalic region low, continuous, with one to three annules. Stylet slender, under 15  $\mu\text{m}$  long, **knobs absent or poorly developed.** Orifice of dorsal oesophageal gland usually more than a quarter stylet length behind stylet base. Postcorpus non-muscular, non-valvate. Basal bulb offset from intestine. Cardia present. Vulval lips not modified; lateral membranes absent; vagina not abnormally thickened. **Postvulval uterine sac present, less than one body width long. Quadricolumella present. Spermatheca axial, round or elongate.** Testis may be reflexed; **sperm small or moderately large.** Spicules tylenchoid. Gubernaculum fixed. Bursa thick, adanal. Tails elongate-conoid.

#### Type genus

*Thada* Thorne, 1941

## Other genus

*Neothada* Khan, 1973

## Note

*Thada* was assigned to Anguininae by Fortuner & Maggenti (1987), who rejected the subfamily Thadinae. A thick, coarsely annulated cuticle and a cardia are not found in members of Anguinoidea. Anguinoids, unlike tylenchoids, have not evolved to have a thick cuticle like that in *Thada* or *Neothada*. Moreover, the cephalic region and amphidial slits and the sperm size are also not similar to those of anguinoids. On the other hand, *Thada* shares many similarities with *Neothada* (note that it was created by splitting *Thada*) and both belong to Thadinae.

## Key to genera of Thadinae

1. Cuticle marked by transverse and longitudinal striae or grooves, spermatheca rounded ..... *Neothada*
- Cuticle marked by transverse striae or grooves only; spermatheca elongate ..... *Thada*

Genus *Thada* Thorne, 1941

(Fig. 24, A–D)

## Diagnosis

Thadinae. Under 1 mm long. **Cuticle coarsely annulated**; annules smooth, 2–3  $\mu\text{m}$  wide. Lateral fields each with four incisures, not areolated. **Cephalic region low**, flattened, with two annules. Amphids with longitudinal slits; framework weakly sclerotized. Stylet delicate, 9–10  $\mu\text{m}$  long, conus one-third as long; slight basal thickenings present. **Orifice of dorsal oesophageal gland about half stylet length behind stylet base. Median bulb non-muscular, non-valvate.** Isthmus elongate. Basal bulb pyriform. Cardia distinct, rounded. Excretory pore just behind hemizonid, at level of deirids, behind nerve ring. Vulva transverse, lips not raised, no lateral membranes. Postvulval uterine sac less than one body width long. **Quadricolumella present. Spermatheca an axial elongated sac.** Ovary outstretched. Rectum and anus distinct. Tail elongate-conoid, tip rounded. Testis tip reflexed; sperm moderately large. Spicules prominently cephalated. Gubernaculum simple. **Bursa adanal, thick**, with smooth margins.

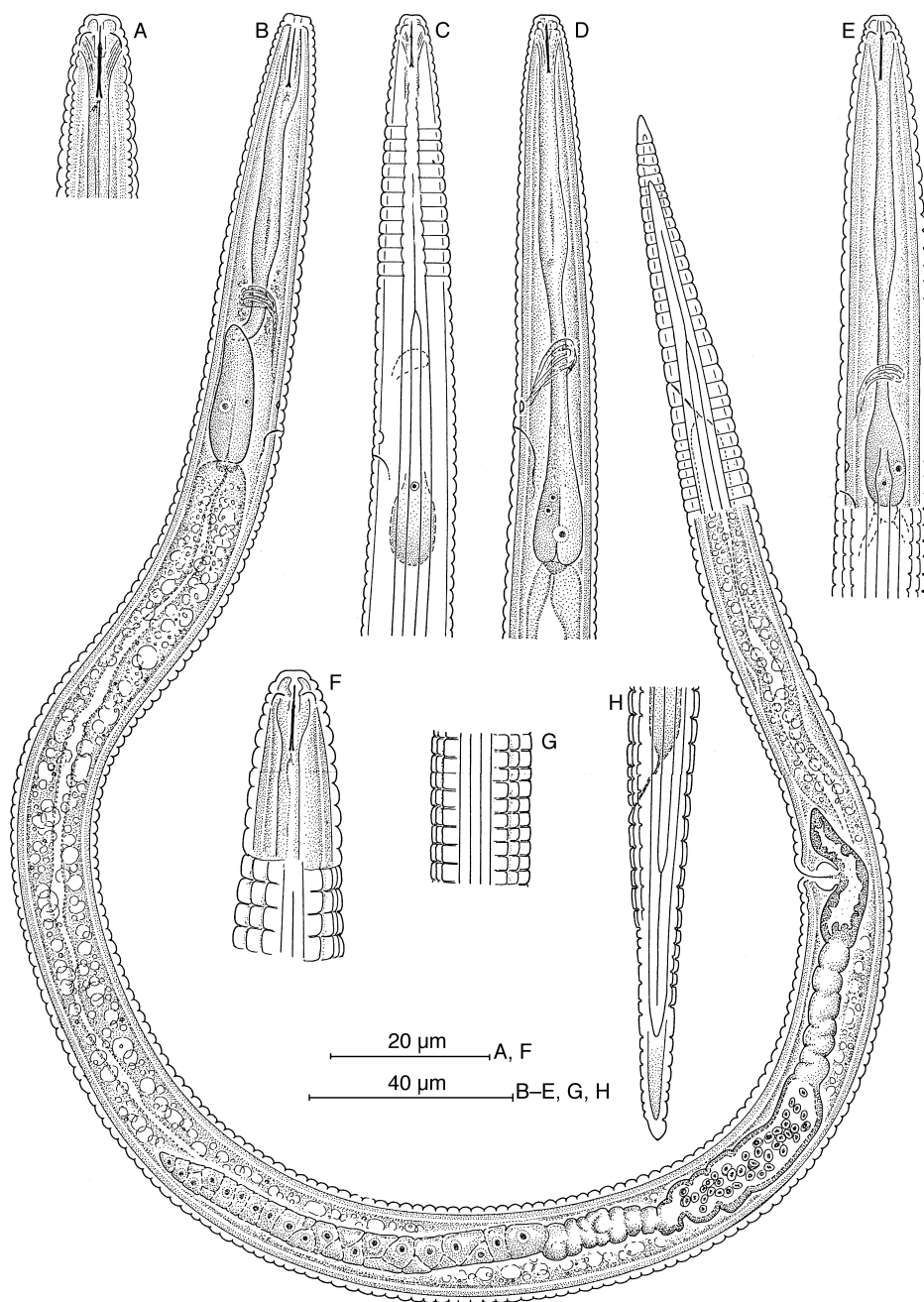
## Type species

*Thada striata* Thorne, 1941

No other species.

ETYMOLOGY. A barbaric word from randomly drawn letters.

*Thada striata* was found around roots of shadscale, *Atriplex confertifolia* and from alfalfa crowns in Utah, USA.



**Fig. 24.** A–D. *Thada striata* Cobb, paratype. E–H. *Neothada cancellata* (Cobb), paratype. A and F. Head ends of female. B. Female. C–E. Oesophageal regions of female. G. Cuticular pattern at midbody. H. Tail end of female.

**Genus *Neothada* Khan, 1973**

(Fig. 24, E–H)

**Diagnosis**

Thadinae. Under 1 mm long. Cuticle tessellated being marked by prominent **coarse transverse and longitudinal striae or grooves dividing the surface into minute squares or rectangular blocks**. Lateral field broad, distinct, with four incisures, not areolated. Cephalic region low, cap-like, continuous, striated. Stylet 8–13  $\mu\text{m}$  long, lacking basal knobs (minute thickenings present in *N. costata*). **Orifice of dorsal gland about one-third or more of stylet length from stylet base**. **Median oesophageal bulb fusiform, non-muscular**. Isthmus elongate-slender. Basal bulb saccate, set off from intestine. Cardia present, generally discoidal. Excretory pore behind nerve ring. Deirids present. Vulva at 61–74%, flush with body contour. Postvulval uterine sac less than one body width long. **Quadricolumella present**. **Spermatheca round, axial**; sperm small. Ovary outstretched; oocytes serially arranged. Tails elongate-conoid, coarsely annulated; tip rounded or pointed. Spicules 13–20.5  $\mu\text{m}$  long. Gubernaculum simple, fixed, 4–6.5  $\mu\text{m}$  long. Bursa adanal.

**Type species**

*Neothada tatra* (Thorne & Malek, 1968) Khan, 1973  
syn. *Thada tatra* Thorne & Malek, 1968

**Other species**

*Neothada andrassyi* Heyns & Van den Berg, 1996  
syn. *N. cancellata* apud Andr  ssy, 1982  
*N. cancellata* (Thorne, 1941) Khan, 1973  
syn. *Thada cancellata* Thorne, 1941  
*N. costata* (Geraert & Raski, 1986) comb. n.  
syn. *Basirienchus costatus* Geraert & Raski, 1986  
*N. geraerti* (Andr  ssy, 1982) Siddiqi, 1986  
syn. *Thada geraerti* Andr  ssy, 1982  
*Neothada geraerti* (Andr  ssy, 1982) Geraert & Raski, 1986  
*Thada cancellata* apud Geraert, 1974  
*N. hades* Heyns & Van den Berg, 1996  
*N. major* Maqbool & Shahina, 1989

**Note**

*Basirienchus costatus* Geraert & Raski, 1986 is closer to *Neothada* than *Basirienchus* because of the presence of cuticular longitudinal ridges all around the body and deep coarse annulation (such annulations and ridges are not found in Boleodorinae where *Basirienchus* belongs) and orifice of dorsal oesophageal gland located about one-third stylet length behind stylet base. Stylet with minute basal thickenings and delicate cuticular thickening in median oesophageal bulb in this species differentiates it from other species of *Neothada*. The species is judged to belong to *Neothada*, to which it is transferred. It resembles *Coslenchus* spp. but differs by the structure of the vulva and vagina and the shape and position of the amphidial apertures outside the labial plate. A key to *Neothada* spp. is given by Heyns & Van den Berg (1996).

ETYMOLOGY. From the Greek *neos* = young, new, and *Thada*.

The type species was found in grass soil in USA.

## Subfamily Duosulciinae Siddiqi, 1979

### Diagnosis

Tylenchidae. Body small (under 1 mm), straight to arcuate upon relaxation, not extremely slender ( $a < 60$ ). **Cuticle deeply annulated; annules distinct, rounded or pointed, may be sculptured; longitudinal and transverse grooves may be present. Lateral field narrow, with a single prominent ridge showing two incisures in lateral view**; in SEM of *Malenchus*, numerous longitudinal lines are seen on this ridge. Prophasms at some distance from lateral ridge, in females a little anterior to vulva (never advulval or postvulval). Amphidial apertures pore-like near oral opening or longitudinal slits originating at top of lateral lips and usually curved ventrally. **Stylet small (less than 15  $\mu\text{m}$ )**, with distinct rounded basal knobs. Orifice of dorsal oesophageal gland closely behind stylet base. Median bulb present or absent. Vulval lips not modified, **lacking lateral membranes**. Vagina straight or curved, directed inward or forward. Spermatheca offset, round, or elongate sac directed forward. Postvulval uterine sac present or absent. Tail elongate-conoid to filiform, with pointed, finely rounded or hooked terminus. Bursa present except in *Miculenchus*, adanal, simple. Cloacal lips elevated but not forming a tube.

### Type genus

*Duosulcius* Siddiqi, 1979

### Other genera

*Allotylenchus* Andr ssy, 1984

*Malenchus* Andr ssy, 1968

Subgenera: *Malenchus* Andr ssy, 1968

*Neomalenchus* Siddiqi, 1979

*Telomalenchus* subgen. n.

*Miculenchus* Andr ssy, 1959

*Mukazia* Siddiqi, 1986

*Ottolenchus* Husain & Khan, 1967

*Ridgellus* gen. n.

*Zanenchus* Siddiqi, 1979

### Key to genera of Duosulciinae

1. Cuticle with longitudinal ridges outside lateral fields ..... *Ridgellus*  
Cuticle without longitudinal ridges outside lateral fields ..... 2
2. Cephalic region dorsoventrally flattened ..... *Malenchus*  
Cephalic region circular ..... 3
3. Cuticle not annulated or striated ..... *Allotylenchus*  
Cuticle annulated ..... 4



4. Annules well separated from each other by grooves; body 0.7 mm or longer ..... *Mukazia*  
Annules contiguous; body under 0.7 mm long ..... 5
5. Body annules prominent, generally sculptured; cephalic region distinctly annulated, with four or more annules ..... 6  
Body annules not prominent or sculptured; cephalic region indistinctly annulated, with less than four annules ..... *Ottolenchus*
6. Postcorpus non-muscular, without refractive thickenings ..... *Duosulcius*  
Postcorpus muscular, with refractive thickenings ..... 7
7. Postvulval uterine sac present; bursa absent ..... *Miculenchus*  
Postvulval uterine sac absent; bursa present ..... *Zanenchus*

### Genus *Duosulcius* Siddiqi, 1979

(Fig. 25)

#### Diagnosis

Duosulciinae. Body slender, straight to arcuate, 0.48–0.66 mm long in type species. **Cuticle deeply annulated; annules distinct, sculptured.** Lateral field with two crenate incisures, very narrow. **Cephalic region continuous, circular, hemispherical, finely striated;** striations continuous with that of the body. Amphidial apertures indistinct. Stylet 6–7  $\mu\text{m}$  long in type species, knobs minutely rounded. Corpus longer than isthmus, **with basal postcorporate swelling devoid of musculature and refractive thickenings.** Isthmus gradually expanding to an elongate-saccate terminal bulb. Vulva at about 64–67% of body length. **Vagina curved, directed forward, its walls strongly sclerotized** in anterior two-thirds. **Postvulval sac absent.** Prothasms less than body width anterior to vulva. Tail elongate-conoid to a sharp point. Male not known.

#### Type species

*Duosulcius acutus* Siddiqi, 1979

#### Other species

*Duosulcius nigeriensis* Talavera & Siddiqi, 1996

ETYMOLOGY. Latin *duo* = two, *sulcus* = furrow (for incisures in lateral fields).

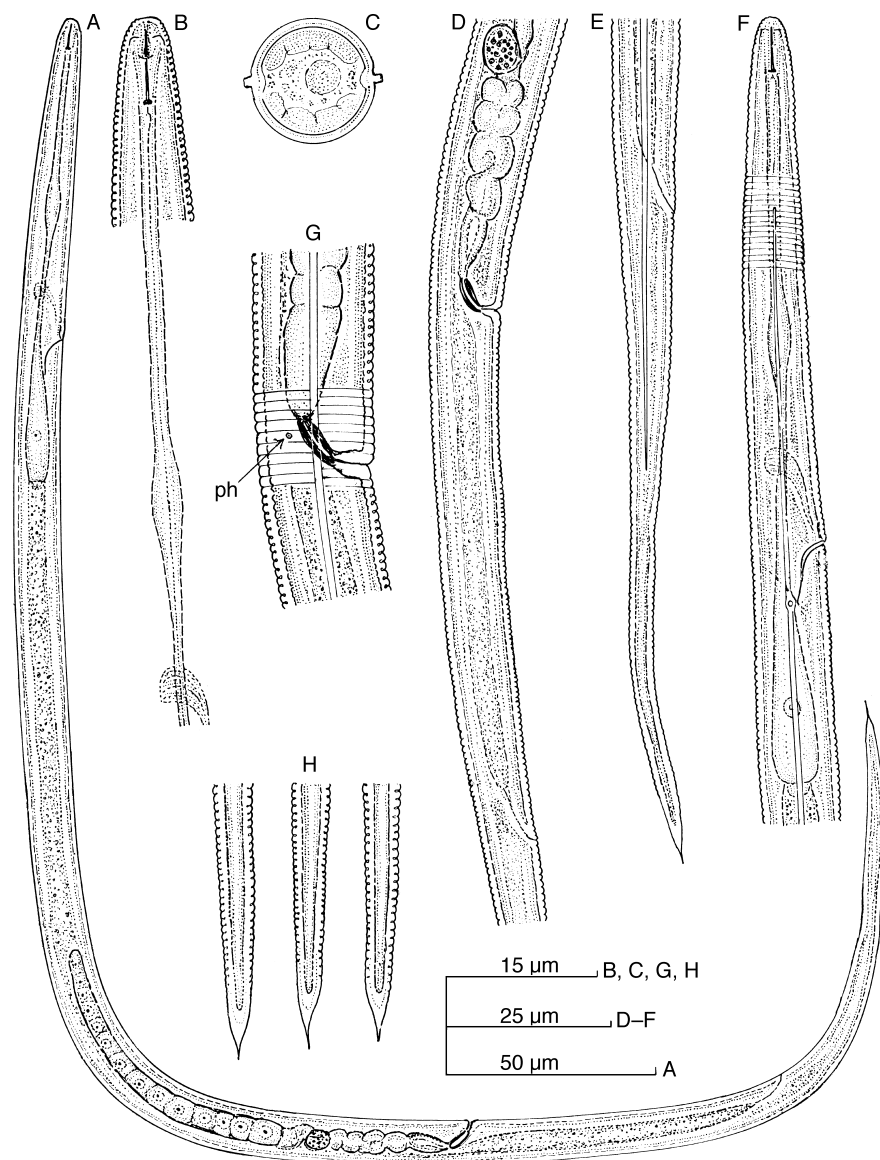
The type species was collected from bush soil at Ibadan, Nigeria. *Duosulcius nigeriensis* was also found near Ibadan, Nigeria in secondary forest soil.

### Genus *Zanenchus* Siddiqi, 1979

(Fig. 26, A–F)

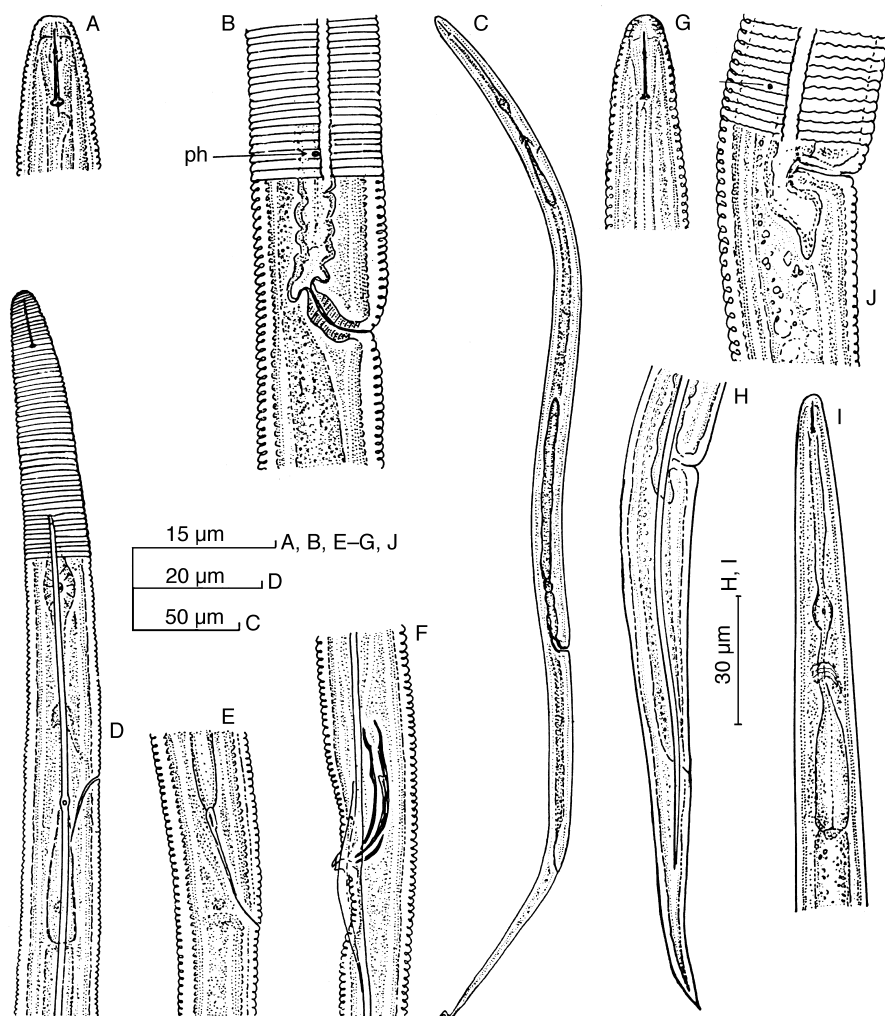
#### Diagnosis

Duosulciinae. Body straight to arcuate, 0.44–0.52 mm long in type species. Cuticle finely but deeply annulated; annules contiguous, may show zig-zag margins.



**Fig. 25.** *Duosulcius acutus* Siddiqi. A, B, D–G. Holotype, remainder paratypes. A. Female. B. Head end. C. Cross-section of body near middle. D. Vulva–anal region. E and H. Tail ends. F. Oesophagus. G. Vulval region showing prothasid (ph). (After Siddiqi (1979a), courtesy *Nematologica*.)

Cephalic region low, continuous with body contour, distinctly annulated, **circular in cross-section**, hemispherical. Amphidial apertures pore-like, indistinct. Stylet 8–9 μm long in type species. **Postcorporate bulb muscular, with distinct refractive thickenings**. Isthmus about as long as precorpus, gradually enlarging to a saccate terminal bulb. Vulva at 61–63% of body length in type species. Vagina curved,



**Fig. 26.** A–F. *Zanenichus zanchus* Siddiqi, A, C and D. Holotype. B, E and F. Paratypes. G–J. *Miculenchus salvus* Andrassy, paratype female. A and G. Head ends. B and J. Vulval regions. C. Female. D and I. Oesophageal regions. E. Anal region. F. Spicular region. H. Posterior region. (After Siddiqi (1979a), courtesy *Nematologica*.)

directed inward and forward, walls thickened, **lightly sclerotized**. **Postvulval uterine sac absent**. Prophasmsids one to two body widths anterior to vulva. Tail elongate-conoid to a hooked or straight tip. Bursa adanal. Spicules tylenchoid, 14–15 µm long in type species. Gubernaculum trough-shaped, fixed, cloacal lips pointed, forming a narrow tube.

#### Type species

*Zanenichus zanchus* Siddiqi, 1979

syn. *Filenichus zanchus* (Siddiqi, 1979) Raski & Geraert, 1987

## Other species

- Zanenchus angustatus* (Brzeski, 1997) comb. n.  
 syn. *Filenchus angustatus* Brzeski, 1997  
*Z. chilensis* (Raski & Geraert, 1987) comb. n.  
 syn. *Filenchus chilensis* Raski & Geraert, 1987  
*Z. linearis* Talavera & Siddiqi, 1996  
*Z. nemorosus* Brzeski, 1986  
 syn. *Filenchus nemorosus* (Brzeski) Raski & Geraert, 1987  
*Z. neonanus* (Raski & Geraert, 1987) comb. n.  
 syn. *Filenchus neonanus* Raski & Geraert, 1987  
*Z. oryzae* Khan & Ahmad, 1991  
*Z. salmae* Siddiqi, 1979 (syn. of *Miculenchus salvus* for Wanless & David, 1997)  
 syn. *Filenchus salmae* (Siddiqi) Raski & Geraert, 1987

## Note

*Filenchus chilensis* and *F. neonanus* have amphidial apertures confined to the labial plate in the front of head, not extending as longitudinal slits along lateral sides of cephalic region, hence their placement under *Zanenchus*. *Filenchus chilensis* fits uneasily in *Zanenchus* because it has a postvulval uterine sac and four incisures in lateral field.

ETYMOLOGY. *Zan* from first three letters of type species name *zanclus*, and Greek *enchos* = spear.

The type species was obtained from soil around roots of Napier grass (*Pennisetum purpureum*) near Tembwe, Malawi.

**Genus *Miculenchus* Andrásy, 1959**

syn. *Tylenchus* (*Miculenchus* Andrásy, 1959) (Goodey, 1963)

***Ceramotylenchus* Ebsary, 1986**

(Fig. 26, G–J)

## Diagnosis

Duosulciinae. Body small (under 0.5 mm), sharply tapering towards extremities, slightly arcuate upon relaxation. Cuticle finely but **distinctly annulated, annules contiguous, sculptured, with fine, zig-zag margins**. Lateral field with single conspicuous ridge. Cephalic region continuous, rounded, body annulations continued to its tip. Amphidial apertures indistinct. Stylet 8–11.5  $\mu\text{m}$  long, with small rounded knobs. **Median bulb small, oval, with refractive thickenings**; basal bulb elongate-saccate. Vulva transverse, depressed, lacking lateral membranes. Vagina thin-walled, roughly at right angles to body axis. Spermatheca small. **Postvulval uterine sac present**. Distance between vulva and anus longer than tail in type species. Tail elongate-conoid, sharply pointed. **Male lacking a bursa**; cloacal aperture overhung by its anterior lip.

## Type species

*Miculenchus salvus* Andrásy, 1959

syn. *Tylenchus* (*Miculenchus*) *salvus* (Andrásy) Goodey, 1963

## Other species

*Miculenchus elegans* Raski & Geraert, 1985 (syn. of *M. salvus* for Brzeski, 1996b)  
*M. tessellatus* (Ebsary, 1986) Maggenti, Luc, Raski, Fortuner & Geraert, 1988  
 syn. *Ceramotylenchus tessellatus* Ebsary, 1986

## Note

*Miculenchus* is interesting in lacking a bursa but the males are rarely reported in the type species. The females are similar in most details, including the zig-zag shape of the annules, to those of *Zanenchus* but differ in having a postvulval uterine sac. *Miculenchus tessellatus* has cuticle bearing small squares arranged in alternating rows and a cup-like perioral disc. These characteristics are not sufficient to treat *Ceramotylenchus* as a separate valid genus.

ETYMOLOGY. From *micu* = a Hungarian pet name, and *lenchus* from *Tylenchus*.

*Miculenchus salvus* was found around roots of rhododendron and *Sesleria* sp. in Capra-Berg, Siebenburgen, Romania.

**Genus *Malenchus* Andr ssy, 1968**

syn. ***Neomalenchus* Siddiqi, 1979**

***Paramalenchus* Sumenkova, 1988**

***Telomalenchus* gen. n.**

## Diagnosis

Duosulciinae. Body elongate-fusiform, with strong and regular tapering behind vulva so that **width at anus becomes about half that at vulva**. Annules prominent as cuticle folds between them. Lateral field with two incisures delimiting single narrow but elevated ridge, which, in SEM, shows 12 or more fine longitudinal lines (subgenera *Malenchus*, *Neomalenchus*), or with four or six incisures making three or five longitudinal bands on most of body (subgenus *Telomalenchus*). **Cephalic region elevated, flattened dorso-ventrally** but not to a great extent, elevated, with four to six fine annules. Labial plate rectangular, bearing four cephalic papillae (pits); amphidial slits curved ventrally and extending for one to two cephalic annules (subgenus *Telomalenchus*) or sinuously for three to five cephalic annules (subgenera *Malenchus*, *Neomalenchus*) along the lateral side of head. Stylet 7–14  $\mu\text{m}$  long, with distinct knobs. Precorpus equal to or shorter than isthmus, postcorpus a muscular bulb with refractive thickenings or lacking musculature (subgenus *Neomalenchus*). Basal bulb pyriform with flat to indented base. **Vulva located in a body cavity**. Spermatheca elongate, oval, or bilobed, offset, directed forward. Vagina straight, not sclerotized, directed inward. Uterus with quadricolumella. Postvulval uterine sac present. Prophasmsids dorso-sublateral, about one body width anterior to vulva. Tail elongate-conoid to a pointed or hooked tip. Bursa adanal. Spicules tylenchoid. Gubernaculum fixed. Cloacal aperture on a cone formed by depression in body at front and rear; lips narrow, pointed.

## Type subgenus

*Malenchus* Andr ssy, 1968, grad. n.

## Other subgenera

*Neomalenchus* Siddiqi, 1979*Telomalenchus* subgen. n.

## Note

Keys to *Malenchus* spp. were given by Andr ssy (1981) and Geraert & Raski (1987).**Key to subgenera of *Malenchus***

1. Postcorpus muscular, with refractive thickenings ..... 2  
    Postcorpus non-muscular, without refractive thickenings ..... *Neomalenchus*
2. Lateral field with two incisures; vulva without lateral membranes ..... *Malenchus*  
    Lateral field with four or six incisures; vulva with lateral membranes  
    ..... *Telomalenchus*

**Subgenus *Malenchus* Andr ssy, 1968, grad. n.**

(Fig. 27, A–F)

## Diagnosis

With the characters of the genus *Malenchus*. Amphidial slits curved ventrally, sinuate, extending for three to five cephalic annules behind labial plate. Lateral field with two incisures delimiting a raised ridge marked by 12 or more fine longitudinal lines. **Median oesophageal bulb muscular, with refractive thickenings.** Vulva in a cavity about two annules wide; lateral membranes absent.

## Type species

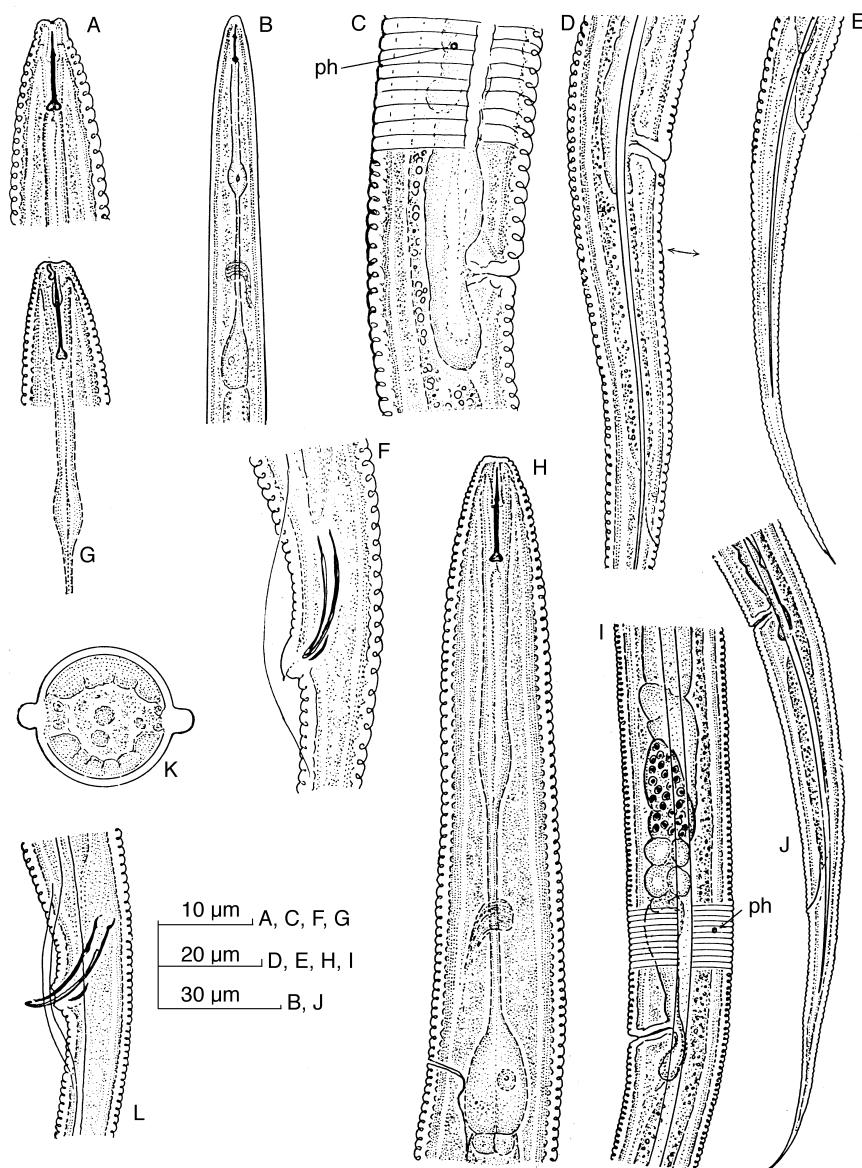
*Malenchus machadoi* (Andr ssy, 1963) Andr ssy, 1968

## Present status

*Malenchus* (*Malenchus*) *machadoi* (Andr ssy, 1963) Andr ssy, 1968syn. *Aglenchus machadoi* Andr ssy, 1963*Tylenchus machadoi* (Andr ssy) Brzeski, 1968

## Other species

*Malenchus* (*Malenchus*) *acarayensis* Andr ssy, 1968syn. *Malenchus cognatus* Andr ssy, 1981*Malenchus eslami* Siddiqui & Khan, 1983*Malenchus moini* Siddiqui & Khan, 1983*Malenchus tantulus* Siddiqui, 1979M. (M.) *adelinae* (Raski & Geraert, 1987) comb. n.syn. *Filenchus adelinae* Raski & Geraert, 1987M. (M.) *andr ssyi* Merny, 1970M. (M.) *angustus* Talavera & Siddiqui, 1996M. (M.) *anthrisulcus* (Sumenkova, 1988) Ebsary, 1991syn. *Paramalenchus anthrisulcus* Sumenkova, 1988M. (M.) *bryanti* Knobloch, 1976M. (M.) *bryophilus* (Steiner, 1914) Andr ssy, 1980



**Fig. 27.** A–F. *Malenchus (Malenchus) machadoi* (Andrássy). A–E. Paratype female. F. Paratype male spicular region. G–L. *Malenchus (Neomalenchus) ovalis* Siddiqi. H–J. Holotype female, G, L. Paratype male. A, B, G and H. Anterior ends. C, D and I. Vulval regions. E and J. Tail ends. F and L. Spicular regions. K. Cross-section of body. (Note prothasmodium (ph) outside lateral field in C and I.) (After Siddiqi (1979a), courtesy *Nematologica*.)

- syn. *Tylenchus bryophilus* Steiner, 1914  
*Tylenchus* (*Aglenchus*) *bryophilus* Steiner, 1914 (Andrássy, 1954)  
*Anguillulina bryophila* (Steiner) Goodey, 1932  
*Aglenchus bryophilus* (Steiner) Meyl, 1961
- M. (M.) *exiguus* (Massey, 1969) Andrásy, 1980  
 syn. *Aglenchus exiguus* Massey, 1969  
*Ottolenchus sulcus* Wu, 1970  
*M. sulcus* (Wu) Siddiqi, 1979  
*Tylenchus sulcus* (Wu) Bello, 1972
- M. (M.) *fusiformis* (Thorne & Malek, 1968) Siddiqi, 1979  
 syn. *Tylenchus fusiformis* Thorne & Malek, 1968  
*Ottolenchus fusiformis* (Thorne & Malek) Wu, 1970
- M. (M.) *gratiosus* Andrásy, 1981
- M. (M.) *holochmatus* (Singh, 1971) Siddiqi, 1986  
 syn. *Tylenchus* (*Tylenchus*) *holochmatus* Singh, 1971
- M. (M.) *kausarae* Khan & Ahmad, 1991 (original name *kausari* emended being female patronym)
- M. (M.) *labiatus* Maqbool & Shahina, 1985
- M. (M.) *laccocephalus* Andrásy, 1981  
 ?syn. *M. pyri* Maqbool & Shahina, 1985
- M. (M.) *macrodorus* Geraert & Raski, 1986
- M. (M.) *nanellus* Siddiqi, 1979
- M. (M.) *neosulcus* Geraert & Raski, 1986  
 syn. *M. sulcus* apud Andrásy, 1981 nec *M. sulcus* (Wu, 1970) Siddiqi, 1979
- M. (M.) *nobilis* Andrásy, 1981
- M. (M.) *pampinatus* Andrásy, 1981
- M. (M.) *paramonovi* Katalan-Gateva & Aleksiev, 1985
- M. (M.) *parvus* Brzeski, 1989
- M. (M.) *platycephalus* (Thorne & Malek, 1968) Andrásy, 1981  
 syn. *Tylenchus platycephalus* Thorne & Malek, 1968  
*Ottolenchus platycephalus* (Thorne & Malek) Siddiqi & Hawsworth, 1982
- M. (M.) *pressulus* (Kazachenko, 1975) Andrásy, 1981  
 syn. *Aglenchus pressulus* Kazachenko, 1975
- M. (M.) *shaheenae* Khan & Ahmad, 1991 (original name *shaheenai* emended being female patronym)
- M. (M.) *solovjovae* Brzeski, 1989
- M. (M.) *subtilis* Lal & Khan, 1988
- M. (M.) *truncatus* Knobloch, 1976
- M. (M.) *undulatus* Andrásy, 1981

ETYMOLOGY. *Ma* from its type species name *machadoi*, and *lenchus* from *Tylenchus*.

The type species was found in moss on trees at Luachimo, Dundo, Angola. A key to species was given by Geraert & Raski (1986a).



**Subgenus *Neomalenchus* Siddiqi, 1979**

(Fig. 27, G–L)

**Diagnosis**

With characters of the genus *Malenchus*. Amphidial slits curved ventrally, sinuate, extending for three to four cephalic annules behind labial plate. Lateral field with two incisures delimiting a raised ridge marked by 12 or more fine longitudinal lines. **Median oesophageal bulb indistinct, non-muscular, without refractive thickenings.** Vulva in a cavity about two annules wide; lateral membranes absent.

**Type species***Neomalenchus ovalis* Siddiqi, 1979**Present status**

*Malenchus* (*Neomalenchus*) *ovalis* (Siddiqi, 1979) Andr ssy, 1981  
syn. *Neomalenchus ovalis* Siddiqi, 1979  
*Malenchus ovalis* (Siddiqi) Andr ssy, 1981

**Other species**

*Malenchus* (*Neomalenchus*) *malawiensis* (Siddiqi, 1979) Andr ssy, 1981  
syn. *Neomalenchus malawiensis* Siddiqi, 1979  
*Malenchus malawiensis* (Siddiqi) Andr ssy, 1981  
*M. (N.) pachycephalus* Andr ssy, 1981  
syn. *Malenchus pachycephalus* Andr ssy, 1981  
*Neomalenchus pachycephalus* (Andr ssy) Siddiqi, 1986

ETYMOLOGY. From Greek *neos* = young, new, and *Malenchus*.

The type species was found around roots of chilli (*Capsicum annum* L.) in Brunei.

**Subgenus *Telomalenchus* subgen. n.**

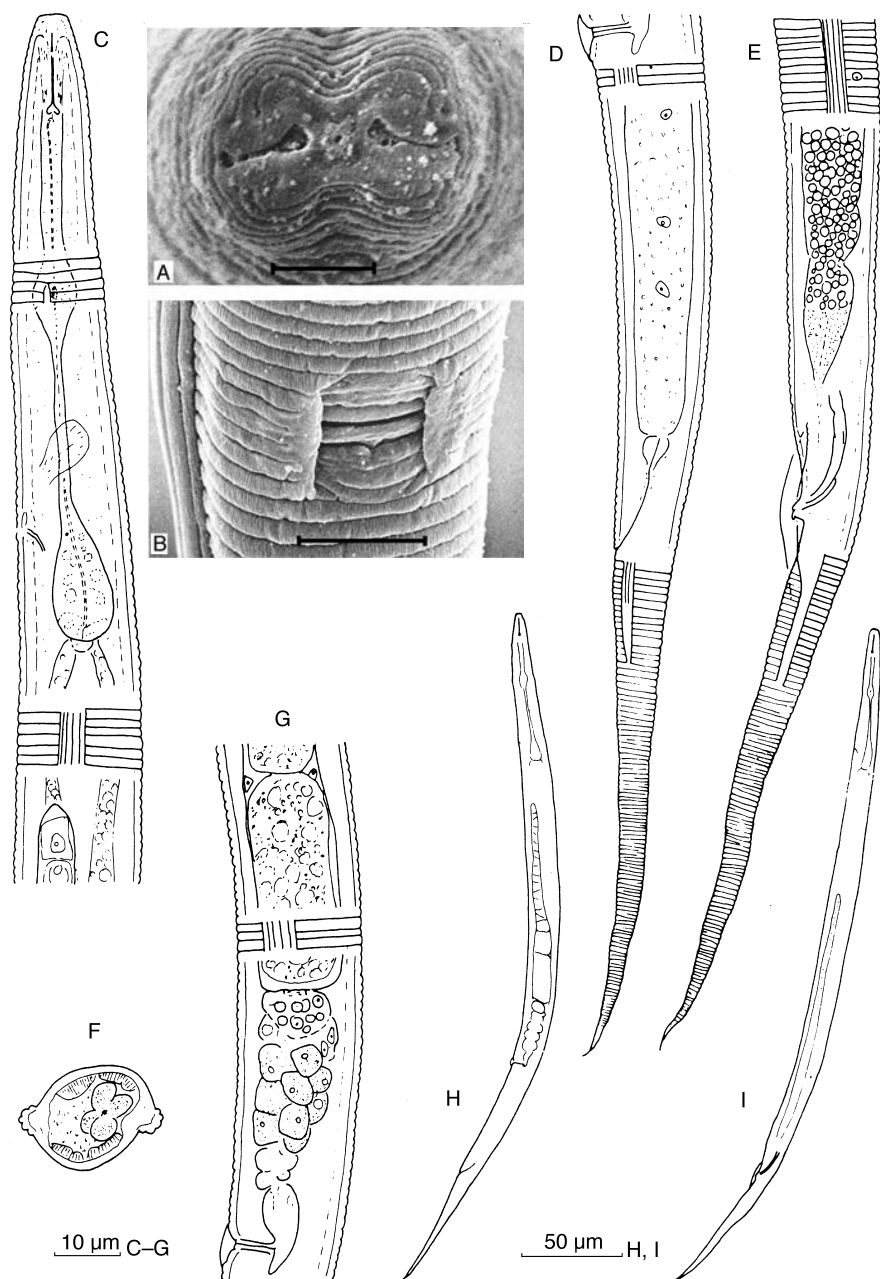
(Fig. 28)

**Diagnosis**

With characters of the genus *Malenchus*. Amphidial slits curved ventrally, extending for one to two cephalic annules behind labial plate. **Lateral field with four or six incisures forming three or five low ridges not marked by longitudinal lines.** Median oesophageal bulb muscular, with refractive thickenings. Vulva in a cavity about four annules wide; **lateral membranes present, prominent.**

**Type species***Telomalenchus williamsi* (Geraert & Raski, 1986) comb. n.**Present status**

*Malenchus* (*Telomalenchus*) *williamsi* Geraert & Raski, 1986  
syn. *Malenchus williamsi* Geraert & Raski, 1986  
*Telomalenchus williamsi* (Geraert & Raski, 1986) comb. n.



**Fig. 28.** *Malenchus (Telomalenchus) williamsi* Geraert & Raski, 1986. E and I. Males, remainder females. A, B. Scanning electron micrographs. A. *En face* view. B. Vulva, ventral view showing large vulval membranes. C. Oesophageal region. D and E. Posterior regions. F. Cross-section of body. G. Reproductive system. H and I. Adults. (After Geraert and Raski (1986), courtesy *Nematologica*.)

## Other species

- Malenchus* (*Telomalenchus*) *leiodermis* Geraert & Raski, 1986  
 syn. *Malenchus leiodermis* Geraert & Raski, 1986  
*Telomalenchus leiodermis* (Geraert & Raski, 1986) comb. n.  
*M. (T.) parthenogeneticus* Geraert & Raski, 1986  
 syn. *Malenchus parthenogeneticus* Geraert & Raski, 1986  
*Telomalenchus parthenogeneticus* (Geraert & Raski, 1986) comb. n.

## Relationship

*Telomalenchus* differs from *Malenchus* in having broader lateral field with four or six incisures, vulva with distinct lateral membranes and shorter amphidial slits (sinuate in *Malenchus*).

ETYMOLOGY. From Greek *telos* = end, and *Malenchus*.

The type species was found in freshwater soil beneath thick tundra at Orange Bay, Hoste Island, Chile. *Malenchus* (*T.*) *leiodermis* and *M. (T.) parthenogeneticus* were found at the same habitat and locality as the type species.

**Genus *Ridgellus* gen. n.**

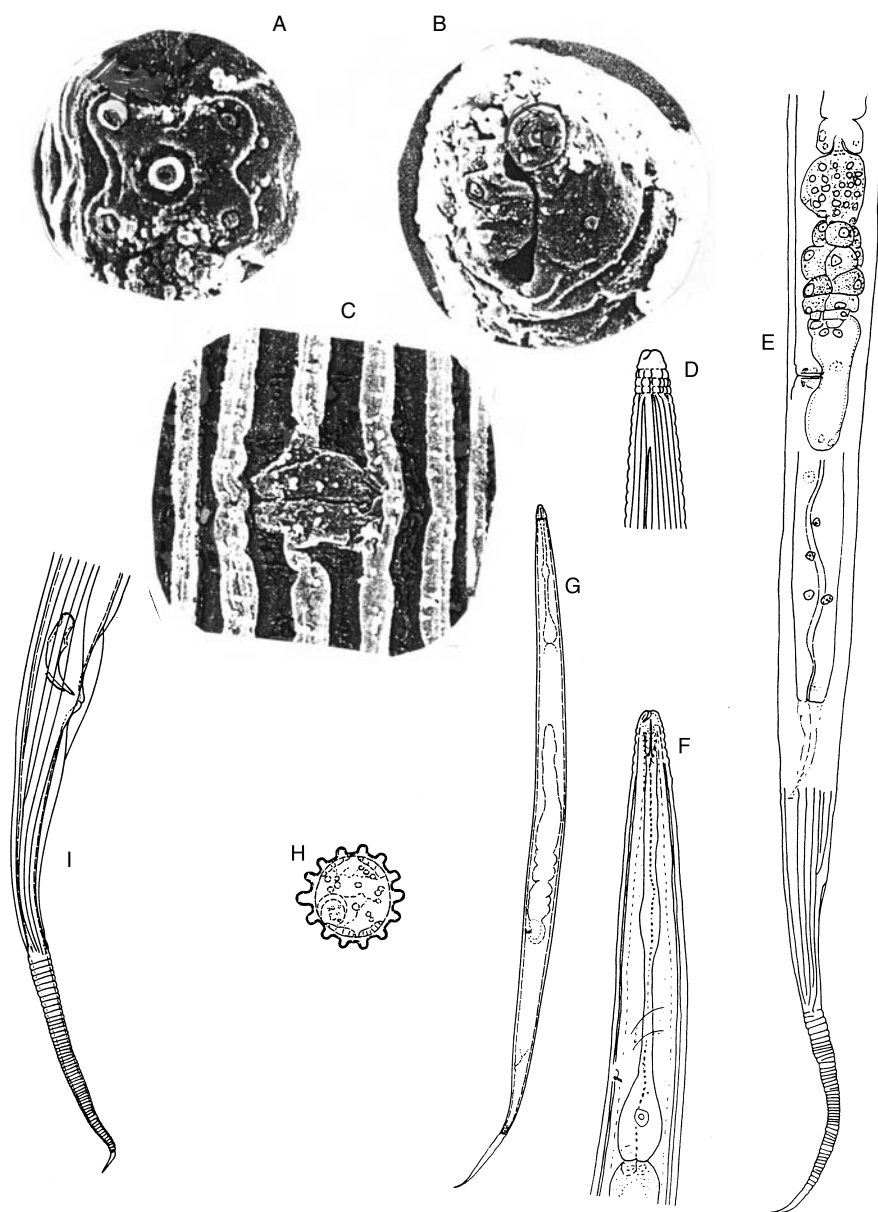
(Fig. 29)

## Diagnosis

Duosulciinae. Body small (0.44–0.53 mm long in type species). **Cuticle with 14 prominent longitudinal ridges not crossed by transverse striae or grooves except near extremities. Lateral field comprises a single ridge slightly higher than others.** Deirids present near excretory pore level. Cephalic region conoid-rounded, high, smooth; labial disc small, raised; labial plate with four lobes, each lobe with a cephalic papilla; amphidial apertures begin near labial disc and extend almost to base of cephalic region as ventrally curved slits which are widened at base; framework not sclerotized. Stylet thin, less than half the length of the precorpus, 9–10  $\mu\text{m}$  long in type species; conus about one-third of its total length; knobs small. Orifice of dorsal oesophageal gland at base of stylet. Oesophagus tylenchoid; **median bulb poorly developed, lacking cuticular thickenings.** Excretory pore located near base of isthmus in type species. Cardia rounded. Vulva a transverse slit at 61–65% of body length in type species; lateral membranes absent. Vagina leading inward, perpendicular to body axis; its walls not thickened. Ovary anteriorly outstretched. Uterus a quadricolumella. Spermatheca subspherical, with small round sperm in type species. Postvulval uterine sac present. Tails elongate-filiform, slightly arcuate ventrally in type species. Male head, stylet and oesophagus as described for female. **Bursa simple, adanal, rudimentary. Cloacal lips rounded, not forming a tube.** Spicules cephalated, pointed, ventrally arcuate, 16–19.5  $\mu\text{m}$  long in type species. Gubernaculum small, fixed.

## Type species

- Ridgellus elenae* (Geraert & Raski, 1986) gen. n., comb. n.  
 syn. *Basirienchus elenae* Geraert & Raski, 1986  
 No other species.



**Fig. 29.** *Ridgellus elenae* (Geraert & Raski, 1986) gen. n., comb. n.. A–C. Scanning electron micrographs. A. *En face* view. B. Head in lateral view showing amphidial slit. C. Vulva and cuticular ridges, ventral view. D. Head end. E. Posterior region of female. F. Oesophageal region of female. G. Female. H. Cross-section of body. I. Posterior region of male. (After Geraert & Raski, 1986, courtesy *Nematologica*.)

## Relationship

*Ridgellus* differs from other Duosulciinae in having longitudinal ridges around the body. It comes close to *Neothada*, from which it differs in having a labial disc, longitudinal ridges not crossed by transverse striae or grooves except near head, stylet having distinct basal knobs and lacking a lateral field, which in *Neothada* has four incisures. The type species is well described and illustrated by Geraert & Raski (1986).

ETYMOLOGY. The generic name is derived from ridge (of the cuticle) and Latin, *ellus* = small, and is masculine in gender.

The type species was found in moist, freshwater soil under deep tundra, Orange Bay, Hardy Peninsula, Hoste Island, Chile.

## Genus *Mukazia* Siddiqi, 1986

(Fig. 30, A–F)

## Diagnosis

Duosulciinae. Body moderately large (female: 0.70–0.86 mm; male 0.9 mm in type species). **Cuticle thick; annules separated, formed by distinct transverse grooves**, interrupted laterally by single ridge forming two incisures. Cephalic region continuous, low, round, distinctly annulated to oral opening. Stylet about one-and-a-half times maximum width of cephalic region (12  $\mu$ m long in type species), with distinct basal knobs. **Median bulb spindle-shaped, poorly muscular, with indistinct refractive thickenings, located behind middle of oesophagus**. Basal bulb enclosing oesophageal glands. Excretory pore opposite basal bulb, just behind hemizonid. Vulval lips not modified. Vagina tubular, directed inward, not sclerotized. **Postvulval uterine sac present**. Spermatheca longitudinally oval, with small round sperm. Ovary outstretched, with less than 15 oocytes. Female tail regularly tapering to a sharply pointed terminus; annules separated from each other up to tail tip. Male tail similar to that of female. **Bursa prominent**, simple, coarsely crenate, adanal. Spicules ventrally arcuate, cephalated, with distal end notched ventrally, 22  $\mu$ m long in type species.

## Type species

*Mukazia nova* (Mukhina & Kazachenko, 1981) Siddiqi, 1986

syn. *Malenchus novus* Mukhina & Kazachenko, 1981

*Malenchus novus* Mukhina, 1981

No other species.

ETYMOLOGY. Derived from names of proposers of its type species: *Muk* from Mukhina, T.I. and *Kaz* from Kazachenko, I.P.

The type species was found in soil around roots of *Echinopanax elatum* Nakai, *Abies nephrolepis* Maxim and *Pinus koraiensis* in the Primorje territory, Far-eastern Russia.

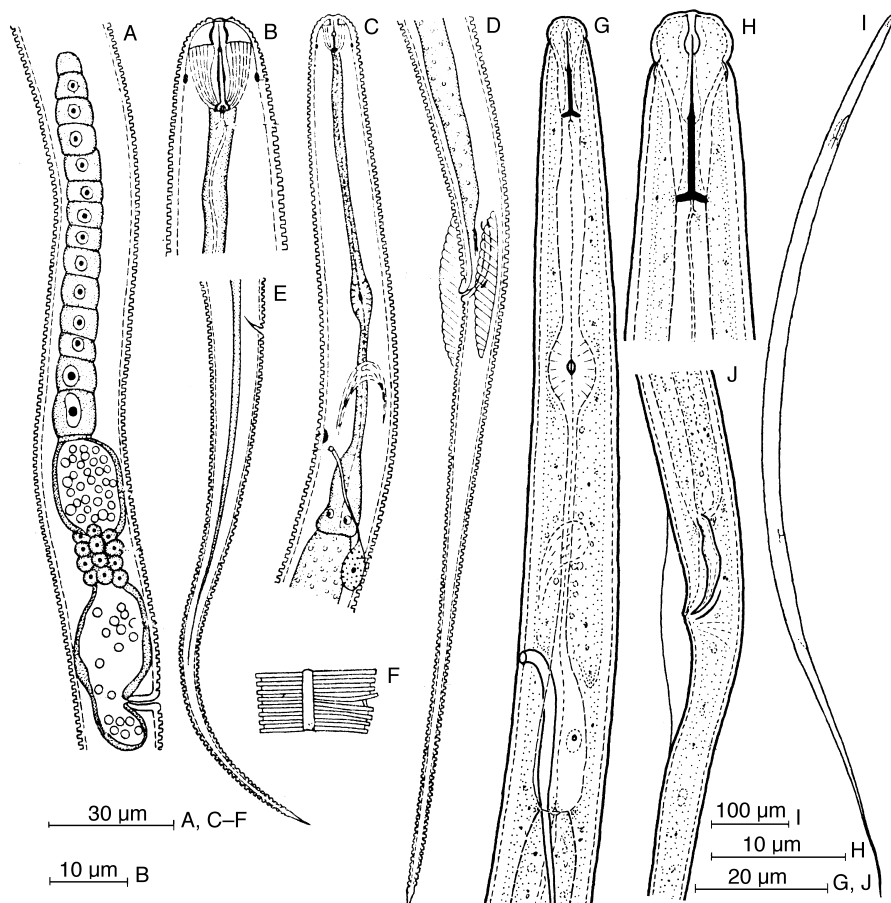


Fig. 30. A–F. *Mukazia nova* Mukhina and Kazachenko. G–J. *Allotylenchus excretorius* Andrassy. A. Reproductive organs of female. B and H. Head ends of females. C and G. Oesophageal region of male and female, respectively. D and E. Tail end of male and female, respectively. F. Annules and lateral field. I. Female. J. Spicular region. (A–F. After Mukhina and Kazachenko, 1981. G–J. After Andrassy, 1984.)

### Genus *Allotylenchus* Andrassy, 1984

(Fig. 30, G–J).

#### Diagnosis

Duosulciinae. Under 1 mm, slender ( $a = 48\text{--}57$ ), almost straight upon relaxation. **Cuticle thin, lacking striation.** Lateral field with a single ridge,  $2\text{--}2.5\text{ }\mu\text{m}$  wide in type species. Cephalic region high, offset, round; amphidial apertures longitudinal slits; framework weak. Stylet weak, knobbed,  $12\text{--}13\text{ }\mu\text{m}$  long in type species. Orifice of dorsal gland close to stylet base. Median bulb muscular, valvate. Basal bulb offset

from intestine. **Excretory pore large; duct wide, heavily sclerotized. Vulva with lateral membranes.** Postvulval uterine sac short. Spermatheca small. Ovary outstretched. Tail elongate-filiform, 210–246  $\mu\text{m}$  long in type species. Bursa adanal, smooth, with symmetrical alae. Spicules 17–19  $\mu\text{m}$  long in type species. Gubernaculum fixed.

#### Type species

*Allotylenchus excretorius* Andr  ssy, 1984

No other species.

ETYMOLOGY. From Greek *allos* = other, and *Tylenchus*.

The type species was found around grass roots at Antibes, France.

#### Genus *Ottolenchus* Husain & Khan, 1967 (Wu, 1970)

syn. *Tylenchus* (*Ottolenchus* Husain & Khan, 1967)

(Fig. 31, A–D)

#### Diagnosis

Duosulciinae. Cuticle with plain, fine or coarse annules not forming loops or folds at junction and hypodermis not distinctly annulated. Lateral field with two incisures bordering a single ridge about one-sixth to one-fifth as wide as body. **Amphidial apertures longitudinal, curved, sinuate, often S-shaped,** originating at lateral lip areas and extending over most of cephalic region. Prophasms dorso-sublateral, one body width or more anterior to vulva. **Cephalic region low, less than three adjacent body annules high, circular in cross-section.** Stylet slender, about 11  $\mu\text{m}$  or less long (mostly between 6 and 8  $\mu\text{m}$ ); conus shorter than shaft; knobs minute, rounded. Postcorpus a muscular bulb with refractive thickenings. Terminal bulb pyriform. Excretory pore and duct often distinct and sclerotized. Vulva flush with body contour or depressed but not forming a cavity, devoid of lateral membranes; lips not modified. Vagina leading inward, not sclerotized. **Postvulval uterine sac present.** Tail elongate-filiform. Bursa adanal. **Spicules slender, slightly arcuate. Gubernaculum slender, linear, not strongly cupped.**

#### Type species

*Ottolenchus equisetus* (Husain & Khan, 1967) Wu, 1970

syn. *Tylenchus* (*Ottolenchus*) *equisetus* Husain & Khan, 1967

*Filenchus equisetus* (Husain & Khan) Raski & Geraert, 1987

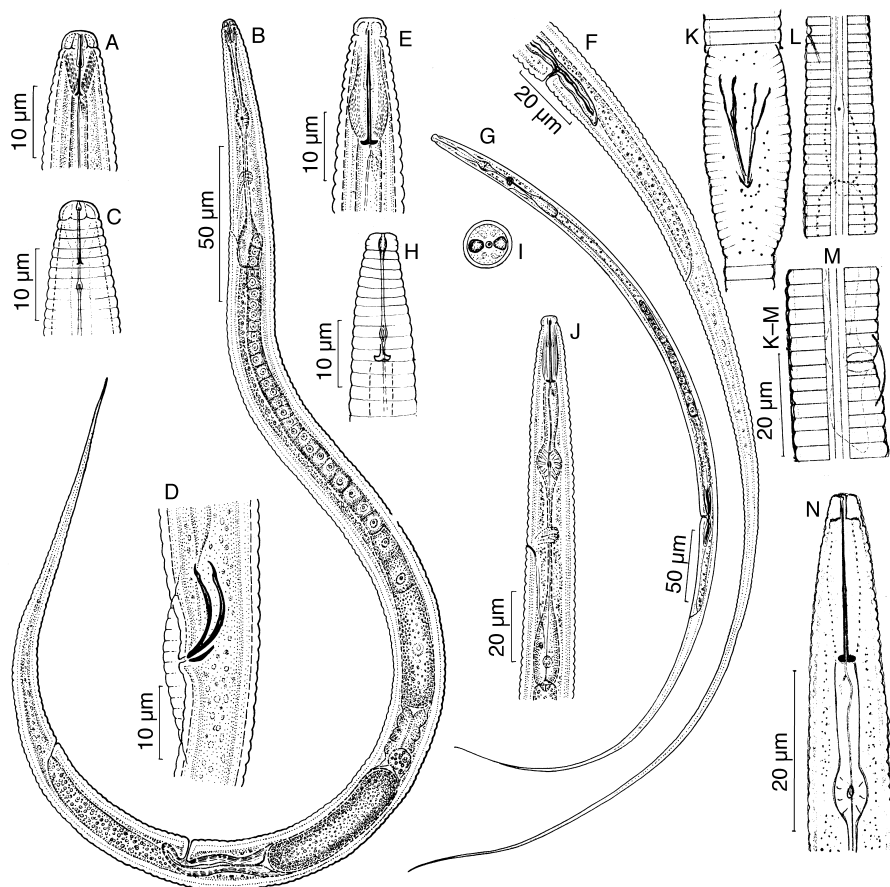
*Tylenchus* (*Aglenchus*) *parvus* Siddiqi, 1963 (= primary homonym of *Tylenchus filiformis* f. *parvus* Micoletzky, 1922)

*Aglenchus parvus* (Siddiqi) Husain, 1967

*Aglenchus parvus* (Siddiqi) Golden, 1971

*Ottolenchus parvus* (Siddiqi) Siddiqi, 1979

*Filenchus neoparvus* Raski & Geraert, 1987 (was a nom. nov. for *T. (A.) parvus* Siddiqi, 1963)



**Fig. 31.** A–D. *Ottolenchus equisetus* (Husain & Khan) (= *Tylenchus parvus* Siddiqi). E–J. *Cephalenchus leptus* (Siddiqi). K–N. *Cephalenchus indicus* (Dhanachand & Jairajpuri). A, C, E, H and N. Head ends of female. B. Female, paratype (of *Tylenchus parvus*). D and K. Bursa regions. F. Posterior end of female. G. Female, holotype. I. Cross-section of head showing sclerotization of amphidial pouches. J. Oesophageal region of female. L. Deirid region. M. Vulval region. (A–J. After Siddiqi (1963b), courtesy Springer Verlag, Heidelberg. K–N. Redrawn after Dhanachand and Jairajpuri (1980).)

### Other species

*Ottolenchus acris* Brzeski, 1986

syn. *Filenchus acris* (Brzeski, 1986) Raski & Geraert, 1987

*Ottolenchus spicatus* Brzeski, 1986 (syn. by Brzeski, 1998)

*Filenchus spicatus* (Brzeski) Raski & Geraert, 1987

*O. balcareanus* (Torres & Geraert, 1996) comb. n.

syn. *Filenchus balcareanus* Torres & Geraert, 1996

*O. cabi* Siddiqi & Hawksworth, 1982

syn. *Filenchus cabi* (Siddiqi & Hawksworth) Raski & Geraert, 1987



- O. callosus* Siddiqi & Lal, 1992  
 syn. *Filenchus callosus* (Siddiqi & Lal) Brzeski, 1997  
*O. cephalatus* Siddiqi & Lal, 1992  
 syn. *Filenchus cephalatus* (Siddiqi & Lal) Brzeski, 1997  
*O. conflexus* Siddiqi & Lal, 1992  
 syn. *Filenchus conflexus* (Siddiqi & Lal) Brzeski, 1997  
*O. crassatus* Siddiqi & Lal, 1992  
 syn. *Filenchus crassatus* (Siddiqi & Lal) Brzeski, 1997  
*O. crassimus* Siddiqi & Lal, 1992  
 syn. *Filenchus crassimus* (Siddiqi & Lal) Brzeski, 1997  
*O. crassistylus* Siddiqi & Lal, 1992  
 syn. *Filenchus crassistylus* (Siddiqi & Lal) Brzeski, 1997  
*O. discrepans* (Andrássy, 1954) Siddiqi & Hawksworth, 1982  
 syn. *Tylenchus (Lelenchus) discrepans* Andrásy, 1954  
     *Lelenchus discrepans* (Andrássy) Meyl, 1961  
     *Filenchus discrepans* (Andrássy) Andrásy, 1972  
     *Filenchus discrepans* (Andrássy) Raski & Geraert, 1986  
     *Tylenchus helenae* Szczygieł, 1969  
     *O. helenae* (Szczygieł, 1969) Brzeski, 1982  
     *O. helenae* (Szczygieł) Siddiqi & Hawksworth, 1982  
     *Filenchus helenae* (Szczygieł) Raski & Geraert, 1987  
*O. dorsalis* (Brzeski, 1997) comb. n.  
 syn. *Filenchus dorsalis* Brzeski, 1997  
*O. facultativus* (Szczygieł, 1970) Brzeski, 1982  
 syn. *Tylenchus facultativus* Szczygieł, 1970  
     *O. facultativus* (Szczygieł) Siddiqi & Hawksworth, 1982  
     *Filenchus facultativus* (Szczygieł) Brzeski, 1982  
     *Filenchus facultativus* (Szczygieł) Raski & Geraert, 1987  
     *Malenchus piauihyensis* Monteiro, 1974  
     *O. piauihyensis* (Monteiro) Siddiqi, 1986  
*O. fortis* Siddiqi & Lal, 1992  
 syn. *Filenchus fortis* (Siddiqi & Lal) Brzeski, 1997  
*O. hamuliger* (Brzeski, 1998) comb. n.  
 syn. *Filenchus hamuliger* Brzeski, 1998  
*O. longibulbus* Siddiqi & Lal, 1992  
 syn. *Filenchus longibulbus* (Siddiqi & Lal) Brzeski, 1997  
*O. longiurus* Siddiqi & Lal, 1992  
 syn. *Filenchus longiurus* (Siddiqi & Lal) Brzeski, 1997  
*O. macramphis* Siddiqi & Lal, 1992  
 syn. *Filenchus macramphis* (Siddiqi & Lal) Brzeski, 1997  
*O. malaysiensis* Siddiqi & Lal, 1992  
 syn. *Filenchus malaysiensis* (Siddiqi & Lal) Brzeski, 1997  
*O. megabulbosus* Siddiqi & Lal, 1992  
 syn. *Filenchus megabulbosus* (Siddiqi & Lal) Brzeski, 1997  
*O. microdentatus* Siddiqi & Lal, 1992  
 syn. *Filenchus microdentatus* (Siddiqi & Lal) Brzeski, 1997  
*O. normanjonesi* (Raski & Geraert, 1987) Siddiqi & Lal, 1992

- syn. *Filenchus normanjonesi* Raski & Geraert, 1987  
*O. paravesiculosus* (Karegar & Geraert, 1998) comb. n.  
 syn. *Filenchus paravesiculosus* Karegar & Geraert, 1998  
*O. porosus* Siddiqi & Lal, 1992  
 syn. *Filenchus porosus* (Siddiqi & Lal) Brzeski, 1997  
*O. pratensis* Sumenkova, 1987  
 syn. *Filenchus pratensis* (Sumenkova) Ebsary, 1991  
*O. ranunculaceus* Sumenkova, 1987  
 syn. *Filenchus ranunculaceus* (Sumenkova) Ebsary, 1991  
*O. recisus* (Grewal, 1991) Siddiqi & Lal, 1992  
 syn. *Filenchus recisus* Grewal, 1991  
*O. trichuris* Siddiqi & Lal, 1992  
 syn. *Filenchus trichuris* (Siddiqi & Lal) Brzeski, 1997  
*O. vesiculosus* (Knobloch & Knierim, 1969) Brzeski, 1982  
 syn. *Tylenchus vesiculosus* Knobloch & Knierim, 1969  
*O. vesiculosus* (Knobloch & Knierim) Siddiqi & Hawksworth, 1982  
*Filenchus vesiculosus* (Knobloch & Knierim) Raski & Geraert, 1987  
*Filenchus vesiculosus* (Knobloch & Knierim) Brzeski, 1982, in Ebsary, 1991

## Remarks

Husain & Khan (1967) proposed *Ottolenchus* as a subgenus of *Tylenchus*, for *Tylenchus* (*Ottolenchus*) *equisetus* Husain & Khan, 1967. Wu (1970) elevated it to genus rank and described *O. sulcus*. Wu's concept of *Ottolenchus* was based on *O. sulcus*, which was regarded by Siddiqi (1979a) to be a species of *Malenchus* Andr ssy, 1968. Golden (1971) synonymized *Ottolenchus* and *O. equisetus* with *Aglenchus* and *Aglenchus parvus* (= *Tylenchus* (*Aglenchus*) *parvus* Siddiqi, 1963), respectively. Siddiqi (1979a) differentiated the genus *Ottolenchus* from *Malenchus* and, accepting Golden's synonymization, considered *O. parvus* (Siddiqi) Siddiqi, 1979 as the type species of *Ottolenchus*. Brzeski (1982) gave a diagnosis of *Ottolenchus* and recognized *O. parvus* as its type species. However, *Tylenchus* (A.) *parvus* Siddiqi, 1963 is a junior primary homonym of *Tylenchus filiformis* f. *parvus* Micoletzky, 1922 and must be rejected (ICZN Articles 53 and 57 (b)). Hence *O. equisetus* becomes a valid species. A key to *Ottolenchus* spp. was given by Brzeski (1982).

The genus *Ottolenchus* can be differentiated from *Filenchus* by the structure of the cephalic region which is low being less than three adjacent body annules high, amphidial apertures ventrally curved and sinuate extending over most of cephalic region (longitudinally straight in *Filenchus*) and a narrow lateral field with two incisures delimiting a single prominent ridge. The cuticular body annules are often coarse and the excretory duct prominent in *Ottolenchus*.

ETYMOLOGY. Named after Gilbert F. Otto, then a member of the Editorial Committee of the *Proceedings of the Helminthological Society of Washington*, in which the description of the genus and its type species was published.

The type species was found around the roots of *Casuarina equisetifolia* at Aligarh, India.

## Subfamily Tanzaniinae subfam. n.

### Diagnosis

Tylenchidae. Body small (under 0.4 mm), ventrally arcuate to C-shaped upon relaxation, not extremely slender ( $a < 40$ ). **Cuticle deeply annulated; annules distinct, rounded, longitudinal grooves divide the cuticle surface into minute squares. Lateral field with a single ridge showing two incisures in middle in SEM.** Prophasms or deirids not seen. Amphidial apertures pore-like near oral opening. **Stylet knobs large and elongated**, aberrant for the family. Orifice of dorsal gland at base of stylet; **orifices of subventral glands about 10  $\mu\text{m}$  behind that of dorsal gland.** **Corpus short and broad, about as long as basal bulb, 1.5 times stylet length;** isthmus elongate-slender; basal bulb saccate. Vulva posterior. **Ovary and testis single, with a few germinal cells.** Vagina directed inward and forward, not sclerotized. **Spermatheca round to oval**, offset dorso-laterally, with small rounded sperm in type species. **Tails elongate-conoid to a small rounded terminus in adults and juveniles.** Male head, stylet and oesophagus as described for female. **Bursa absent.** Spicules tylenchoid. Gubernaculum small, fixed.

### Type genus

*Tanzanius* Siddiqi, 1991

No other genus.

## Genus *Tanzanius* Siddiqi, 1991

(Fig. 32)

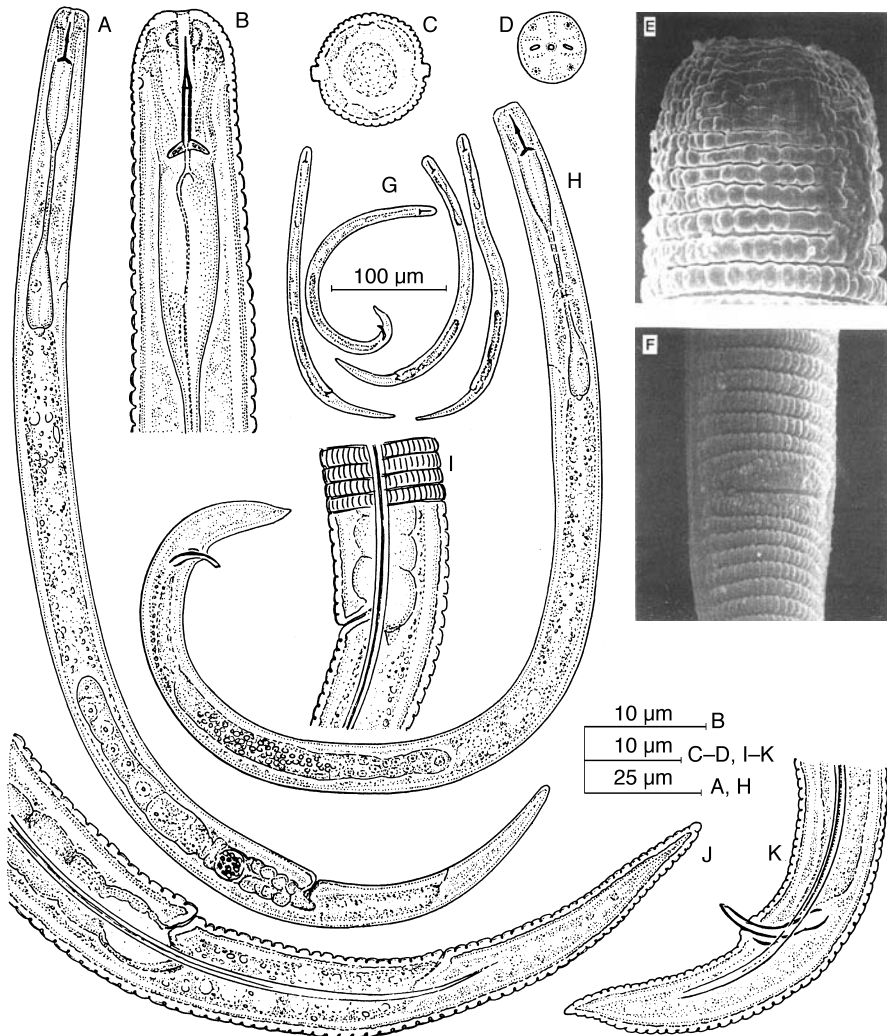
### Diagnosis

With characters of Tanzaniinae. Body small, under 0.33 mm long, ventrally arcuate upon relaxation;  $a = 22\text{--}30$  in type species. **Cuticle strongly annulated and tessellated**, marked by transverse and longitudinal grooves. **Lateral field a single narrow ridge.** Cephalic region broadly rounded, continuous, minutely striated, in SEM surface ornamented with minute squares or circles; four cephalic papillae raised above surface. Amphid apertures close to oral opening, not detectable in lateral view. Deirids and prophasms not seen. Stylet about 10  $\mu\text{m}$  long, **knobs large, abnormally elongated, flanged.** Orifice of dorsal gland at base of stylet; **orifices of subventral glands about one stylet length behind that of dorsal gland.** Excretory pore behind nerve ring. Cardia rounded. Vulva posterior. **Ovary with less than ten oocytes.** Vagina directed inward and forward, not sclerotized. Glandular part of uterus a tricolumella. Spermatheca with small rounded sperms. Postvulval uterine sac rudimentary. **Tails elongate-conoid to a small rounded terminus in adults and juveniles.** Male head, stylet and oesophagus as described for female. Male tail short, subcylindroid to a conoid tip. **Testis single, with a few spermatogonia; numerous small rounded sperm in vas deferens.** **Bursa absent.** Spicules tylenchoid, ventrally arcuate with subterminal pore located ventrally, 11.5–12.5  $\mu\text{m}$  long in type species. Gubernaculum small (3–4  $\mu\text{m}$  long in type species), fixed.

### Type species

*Tanzanius coffeae* Siddiqi, 1991

No other species.



**Fig. 32.** *Tanzanius coffeae* Siddiqi, 1991. A. Female. B. Head end of female. C. Cross-section of body. D. En face view. E, F. Scanning electron micrographs. E. Head end. F. Vulval region. G. Adults. H. Male. I. Vulval region. J. Posterior region of female. K. Posterior region of male. (After Siddiqi (1991), courtesy *Afro-Asian Journal of Nematology*.)

### Note

*Tanzanius* is unique in Tylenchidae in the shape and structure of the stylet and corpus and location of the orifices of subventral oesophageal glands only about 10 µm from that of the dorsal gland. The genus shows affinities to members of the Duosulciinae in the cuticle and lateral field structure, in having similar reproductive organs, and in male lacking a bursa as in *Miculenchus*. In having strongly annulated and tessellated cuticle it shows resemblance to *Neothada* and in small body size, broad corpus and tail shape to the genus *Paratylenchus* of the Criconeematina.

ETYMOLOGY. The generic name is derived from Tanzania, the country where the type species was found, and is masculine in gender.

The type species was found in soil around roots of *Coffea arabica* in Kilimanjaro foothills near Lyamungo Research Station, Tanzania. I have also identified it from forest soil samples from Korup and Mbalmayo forest reserves in Cameroon.

## FAMILY ECPHYADOPHORIDAE

(Extremely attenuated Tylenchoidea, with cylindroid corpus, small stylet and lobed bursa)

These nematodes are so remarkably slender as to appear fibre-like and are easily overlooked (unless they are searched for). They have a maximum width of about 10–12  $\mu\text{m}$  and the cuticle is smooth and relatively thick when compared to what it encloses and this gives them a glassy appearance.

The attenuation of the body, an undifferentiated corpus and lobed bursa are the most important features of the members of this family. These nematodes have undergone further modification such as the enlargement of the amphidial apertures and the dorsal gland extending over the intestine, abrupt tapering of the male body behind the anal region, and modifications in vulval and cloacal lip structure. The stylet is small and the oesophagus is typically tylenchoid, having a slender isthmus and a basal bulb, but the overlapping glandular lobe and cylindroid corpus give a false impression of a Hexatylinina-type oesophagus. It is only the dorsal gland that projects out of the bulb and forms a lobe over the intestine – a condition also found in other tylenchid genera (*Epicharinema*).

The type genus *Ecphyadophora* has a circular cephalic region base in cross-section, pore-like amphids and four incisures in the lateral field, while *Tenunemellus* is different in these respects. *Tenunemellus*, *Ecphyadophoroides* and *Mitranema* have a single lateral ridge and appear to have been derived from a *Duosulcius*-like ancestor, by the greater attenuation of the body. In contrast, *Ecphyadophora*, with a different type of lateral field and almost straight spicules directed backwards, perhaps originated from a different stock. A recently described genus, *Tremonema* Siddiqi, 1994, lacks a lateral field but the cuticle is deeply annulated and the bursa is lobed as in *Mitranema*. *Ultratenella* is similar to *Ecphyadophora* in having a greatly attenuated body, a rounded cephalic region, and vulva facing backward, but it has a simple bursa which is not lobed (see Siddiqi, 1994). Thus the family is quite heterogeneous in composition.

## Family Ecphyadophoridae Skarbilovich, 1959

### Diagnosis

Tylenchoidea. **Body small (under 1 mm), extremely slender, attenuated** and appearing glass fibre-like (maximum width generally 8–10  $\mu\text{m}$ ; **a = 60–181**). Cuticle thin, smooth or moderately thick and deeply annulated. Lateral fields each with two to four incisures, may be obscure or absent. Cephalic region circular or dorsoventrally flattened, continuous with body contour. Four cephalic papillae on surface, but not projecting as setae. Amphidial apertures pore-like, near oral opening,

or longitudinal clefts occupying most of lateral contour of cephalic region. Prophasms postmedian, dorso-sublateral, in females just anterior to vulva. **Stylet short** (15  $\mu\text{m}$  or less), attenuated, with needle-like solid-appearing tip of conus and small round basal knobs. Corpus cylindroid, non-muscular, **lacking a postcorporal bulb**. Basal bulb present but dorsal gland may extend as lobe over intestine. Vulva transverse, posterior, may be covered with anterior lip flap. Vagina directed inward or forward. Postvulval uterine sac present. Spermatheca offset. Tails very long, filiform. Testis single, short. Sperm minute, rounded. **Bursa adanal, lobed projecting outward and backward**, or simple flap-like (*Ultratenella*). Spicules needle-like, setose or tylenchoid. Gubernaculum present, fixed, may be obscure. Cloacal lips pointed or more elongated to form a penial tube. Hypopygium absent.

#### Type subfamily

Ecphyadophorinae Skarbilovich, 1959

#### Other subfamily

Ecphyadophoroidinae Siddiqi, 1986

#### Key to subfamilies of Ecphyadophoridae

1. Amphidial apertures long, slit-like, extending to middle or more of cephalic region; vulva directed outward; not overhung by its anterior lip; spicules arcuate, tip pointing ventrally ..... **Ecphyadophoroidinae**  
 Amphidial apertures indistinct, pore-like vulva directed posteriorly, overhung by its anterior lip; spicules almost straight, tip pointing posteriorly ..... **Ecphyadophorinae**

#### Subfamily Ecphyadophorinae Skarbilovich, 1959

##### Diagnosis

Ecphyadophoridae. Body abruptly narrowed behind vulva and base of penial tube. Cuticle thin, smooth. Lateral field with four incisures, or obscure. **Cephalic region hemispherical, continuous with body contour. Amphidial apertures pore-like, indistinct. Vulva directed posteriorly, overhung by its anterior lip flap.** Vagina curved, sigmoid, directed forward and inward. Bursa adanal, flaps rather rectangular and projecting outward and backward, or simple. **Spicules almost straight**, setose, pointed, tip directed backward. Gubernaculum indistinct. Cloacal lips forming a penial tube directed backward in type species.

##### Type genus

*Ecphyadophora* de Man, 1921

##### Other genus

*Ultratenella* Siddiqi, 1994

### Key to genera of Ecphyadophorinae

1. Body constricted behind vulva and cloacal aperture; dorsal oesophageal gland extending over intestine; bursa lobed ..... *Ecphyadophora*  
 Body not constricted behind vulva and cloacal aperture; dorsal oesophageal gland enclosed in basal bulb; bursa simple, not lobed ..... *Ultratenella*

### Genus *Ecphyadophora* de Man, 1921

syn. *Karachinema* Maqbool & Shahina, 1985

(Fig. 33)

#### Diagnosis

Ecphyadophorinae. **Body abruptly narrowed behind vulva and base of penial tube.** Cuticle appearing smooth but marked with transverse striae. **Lateral field with four incisures.** **Cephalic region continuous, circular, lacking labial disc.** Corpus cylindrical, lacking bulb or refractive thickenings. **Dorsal gland forming a long lobe over intestine.** Oesophago-intestinal junction obscure. Vulva directed posteriorly, with a flap-like anterior lip covering it, lacking lateral membranes. Postvulval uterine sac short. **Spicules needle-like, almost straight.** Gubernaculum present or absent. **Cloacal lips forming characteristic penial tube directed posteriorly.** Bursa with long rather squarish lobe directed posteriorly.

#### Type species

*Ecphyadophora tenuissima* de Man, 1921

syn. *E. tarjani* Husain & Khan, 1965 (= sp. inq. in Raski *et al.*, 1982)

#### Other species

*Ecphyadophora basiri* Verma, 1972

syn. *E. tritici* Verma, 1972

*E. caelata* Raski & Geraert, 1986

*E. elongata* (Maqbool & Shahina, 1985) Geraert & Raski, 1987

syn. *Karachinema elongatum* Maqbool & Shahina, 1985

*E. goodeyi* Husain & Khan, 1965

*E. quadralata* Corbett, 1964

syn. *E. acuta* Husain & Khan, 1968

*E. acuta* Khan, 1972 (in *Helm. Abstr. (B)* 43, No. 808)

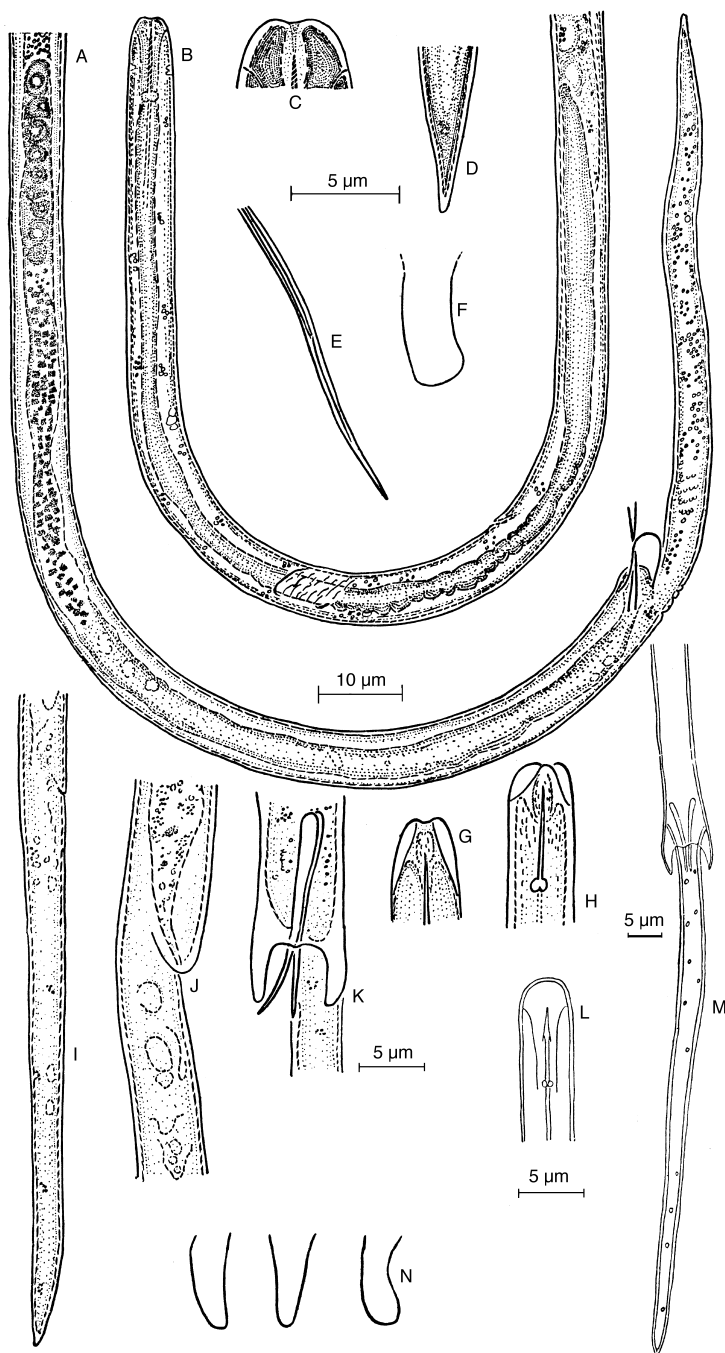
*E. teres* Raski, Koshy & Sosamma, 1982

*E. vallipuriensis* Husain & Khan, 1968

syn. *E. vallipuriensis* Khan, 1972 (in *Helm. Abstr. (B)* 43, No. 808)

ETYMOLOGY. From Greek *ekphyas* (genitive *ekphyados*) = protuberance, process, and *phoros* = bearer (for projecting cloacal lips or for bursa).

The type species was collected from forest soil covered with vegetation near Breda, Holland. Raski *et al.* (1982) gave a key to *Ecphyadophora* spp.



**Fig. 33.** *Ecpyadophora tenuissima* de Man. A and M. Posterior regions of males. B. Anterior region of male. C, G and L. Head ends of males. D. Tail end of male. E. Spicule. F. Bursa. H. Head end of female. I. Tail end of female. J. Vulval region. K. Spicular region. N. Tail tips. (A–K and N. After Tarjan (1957), courtesy *Nematologica*. L and M. After de Man (1921).)



**Genus *Ultratenella* Siddiqi, 1994**

(Fig. 34)

**Diagnosis**

Ecphyadophorinae. Body exceedingly thin ( $a > 120$ ), straight to slightly arcuate ventrally upon relaxation, 0.78–0.94 mm long in type species. **Cuticle thin, smooth. Lateral field absent.** Deirids and prophasms not seen. Cephalic region rounded, continuous; circular in cross-section; amphids, perioral disc and papillae not detectable; framework not sclerotized. Stylet thin, under 10  $\mu\text{m}$  long; conus about one-third of total stylet length; knobs tiny. Orifice of dorsal oesophageal gland at base of stylet. **Oesophagus tylenchoid but lacking median bulb.** Precorpus and isthmus elongate-slender; basal bulb elongate, offset from intestine. Excretory pore not located. Hemizonid behind nerve ring. Cardia small, rounded. Vulva a transverse **slit facing backward, overhung by its anterior lip**, at 60–66% of body in type species; lateral membranes absent. **Vagina sigmoid leading inward and forward**, its walls not sclerotized. Ovary anteriorly outstretched. Spermatheca longitudinally oval, with small rounded sperm in type species. Uterus very long as compared to body width. **Postvulval uterine sac absent. Tails elongate-filiform, straight.** Male head, stylet and oesophagus as described for female. **Bursa simple, adanal, with round smooth margins, not lobed.** Spicules pointed, almost straight, 9–10  $\mu\text{m}$  long in type species. Gubernaculum not seen.

**Type species***Ultratenella vitrea* Siddiqi, 1994

No other species.

**Note**

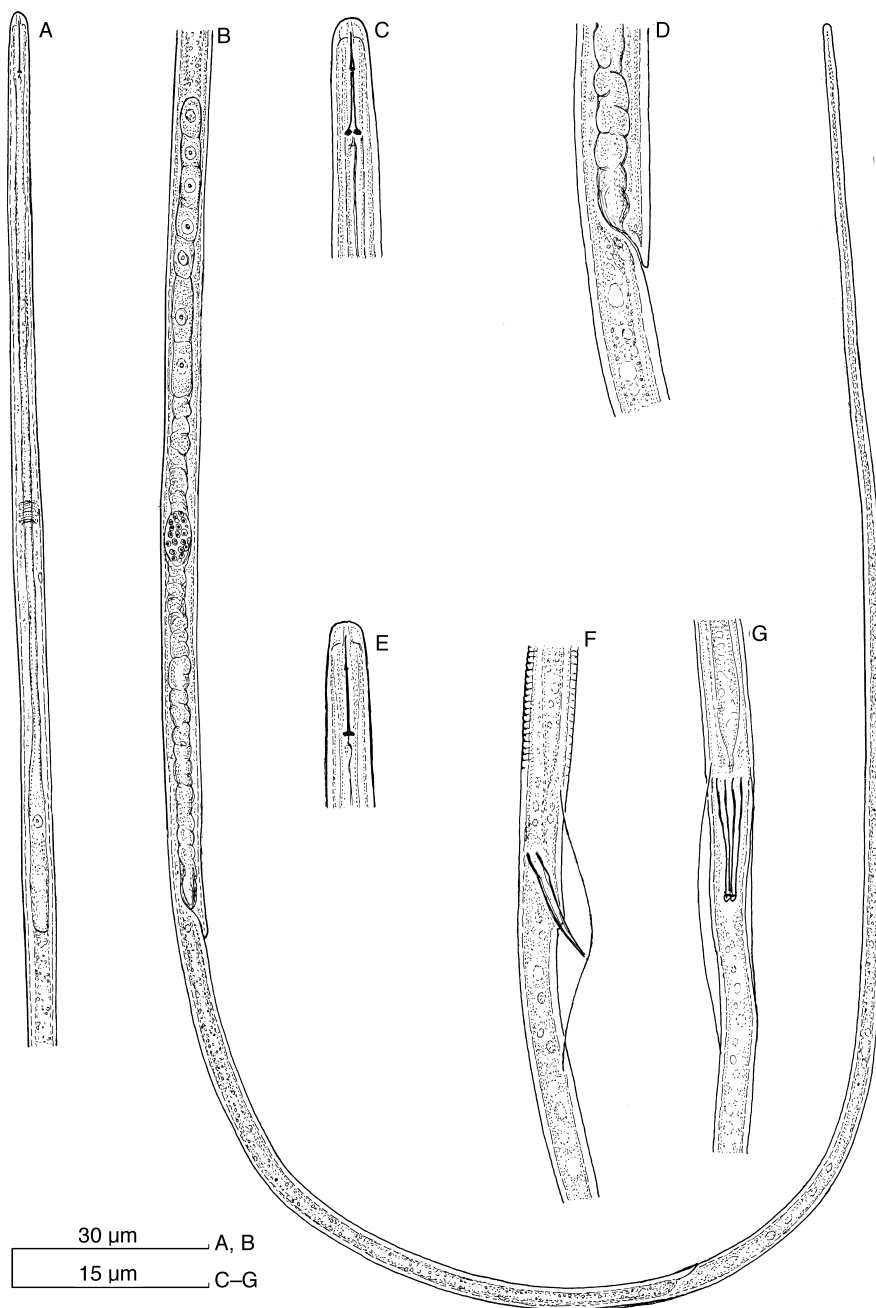
*Ultratenella* is unique in the family in not having a lobed bursa. In other characters, especially the slenderness of the body and head shape, it is similar to *Ecphyadophora*.

ETYMOLOGY. The generic name is derived from Latin, *ultra* = extreme, and *tenella* = diminutive of *tener* = thin and refers to the ultrathin body.

The type species was found in soil around roots of a forest tree, *Mitragyna ciliata* in Korup National Park, Ndian Division, South-West Province, Cameroon.

**Subfamily Ecphyadophoroidinae Siddiqi, 1986****Diagnosis**

Ecphyadophoridae. Cuticle thick, usually strongly annulated. **Body not abruptly narrowed behind vulva and cloacal lips. Lateral field with one to two ridges**, rarely obscure or absent (*Tremonema*). Cephalic region high with cleft-like amphidial apertures, or low with pore-like amphidial apertures. **Vulval and cloacal apertures facing outwards. Vulva not overhung by its anterior lip**, lateral membranes present or absent. Vagina directed inward. Bursa lobed, flaps rectangular or anteriorly convex, posteriorly concave, projecting outward and backward. **Spicules ventrally arcuate, pointed, tip directed ventrally.** Gubernaculum distinct, rod- or trough-like, fixed.



**Fig. 34.** *Ultratenella vitrea* Siddiqi, 1994. A. Oesophageal region of female. B. Posterior region of female. C. Head end of female. D. Vulval region. E. Head end of male. F and G. Spicular region, lateral and ventral view, respectively. (After Siddiqi (1994), courtesy *Afro-Asian Journal of Nematology*.)

## Type genus

*Ecphyadophoroides* Corbett, 1964

## Other genera

*Chilenchus* gen. n.

*Lelenchus* Andrásy, 1954

*Mitranema* Siddiqi, 1986

*Tenunemellus* Siddiqi, 1986

*Tremonema* Siddiqi, 1994

**Key to genera of Ecphyadophoroidinae**

1. Cephalic region flattened dorsoventrally; amphidial apertures distinct as longitudinal clefts running along most of head region ..... 2  
 Cephalic region circular; amphidial apertures indistinct, pore-like, near oral aperture ..... 5
2. Cuticle bearing longitudinal ridges all around body; vulva without lateral membranes; cloacal lips forming a penial tube ..... *Ecphyadophoroides*  
 Cuticle lacking ridges all around body; vulva with lateral membranes; cloacal lips not forming a penial tube ..... 3
3. Stylet without basal knobs or thickenings; oocytes in multiple rows; spicules angular ..... *Chilenchus*  
 Stylet with basal knobs; oocytes in single row; spicules arcuate ..... 4
4. Median oesophageal bulb muscular; bursa simple with convex margins ..... *Lelenchus*  
 Median oesophageal bulb non-muscular; bursa rectangular ..... *Tenunemellus*
5. Lateral field and perioral disc present ..... *Mitranema*  
 Lateral field and perioral disc absent ..... *Tremonema*

**Genus *Ecphyadophoroides* Corbett, 1964**

(Fig. 35, A–I)

## Diagnosis

Ecphyadophoroidinae. **Cuticle bearing longitudinal ridges all around body** for most of its length and **which are crossed by transverse grooves to form rectangular blocks** except in lateral fields. **Lateral fields with a single ridge forming two incisures.** Cephalic region strongly flattened dorso-ventrally; anterior end bottle-shaped in lateral view; labial disc absent. Amphidial apertures longitudinal clefts running along most of lateral cephalic contour. Stylet about 10 µm long, with small knobs. Corpus cylindroid. Isthmus slender. Basal bulb enclosing oesophageal glands. Deirids a little behind level of excretory pore. **Vulva transverse, lips pointed, lacking lateral membranes.** Tail elongate-conoid, pointed. Bursa adanal, flaps rather rectangular, projecting outward and backward. Spicules tylenchoid. Gubernaculum linear, fixed. Cloacal lips forming a short penial tube.

## Type species

*Ecphyadophoroides annulatus* Corbett, 1964

## Other species

*Ecphyadophoroides theae* Eroshenko & Nguen Vu Thanh, 1981

ETYMOLOGY. From *Ecphyadophora*, and *oides* = likeness, similar.

The type species was found on roots of *Fimbristylis* sp. growing in waterlogged grass-land near the Outer Circular Road, Zomba Mountain, Malawi.

**Genus *Tenunemellus* Siddiqi, 1986**

(Fig. 35, J–N)

## Diagnosis

Ecphyadophoroidinae. Cuticle finely or coarsely striated, **lacking longitudinal ridges. Lateral field obscure. Cephalic region strongly flattened dorsoventrally**, lacking labial disc. **Amphidial apertures longitudinal clefts** running along most of lateral contour of cephalic region. Corpus cylindroid. Basal bulb enclosing glands; **dorsal gland may form a short lobe**. Vulva flush with body contour, usually with lateral membranes; lips not modified. Tail very long, pointed. Spicules tylenchoid, cephalated, ventrally arcuate. Gubernaculum present. Bursa flaps rectangular, lobed, projecting outward and backward. Cloacal lips pointed, not forming a penial tube.

## Type species

*Tenunemellus tenuis* (Corbett, 1964) Siddiqi, 1986

syn. *Ecphyadophoroides tenuis* Corbett, 1964

## Other species

*Tenunemellus graminis* (Husain & Khan, 1968) Siddiqi, 1986

syn. *Ecphyadophoroides graminis* Husain & Khan, 1968

*T. indicus* (Verma, 1972) Siddiqi, 1986

syn. *Ecphyadophoroides indicus* Verma, 1972

*T. leptcephalus* (Raski, Koshy & Sosamma, 1982) Siddiqi, 1986

syn. *Ecphyadophoroides leptcephalus* Raski, Koshy & Sosamma, 1982

*T. macrocephalus* (Raski, Koshy & Sosamma, 1982) Siddiqi, 1986

syn. *Ecphyadophoroides macrocephalus* Raski, Koshy & Sosamma, 1982

*T. sheri* (Raski, Koshy & Sosamma, 1982) Siddiqi, 1986

syn. *Ecphyadophoroides sheri* Raski, Koshy & Sosamma, 1982

## Species inquirenda

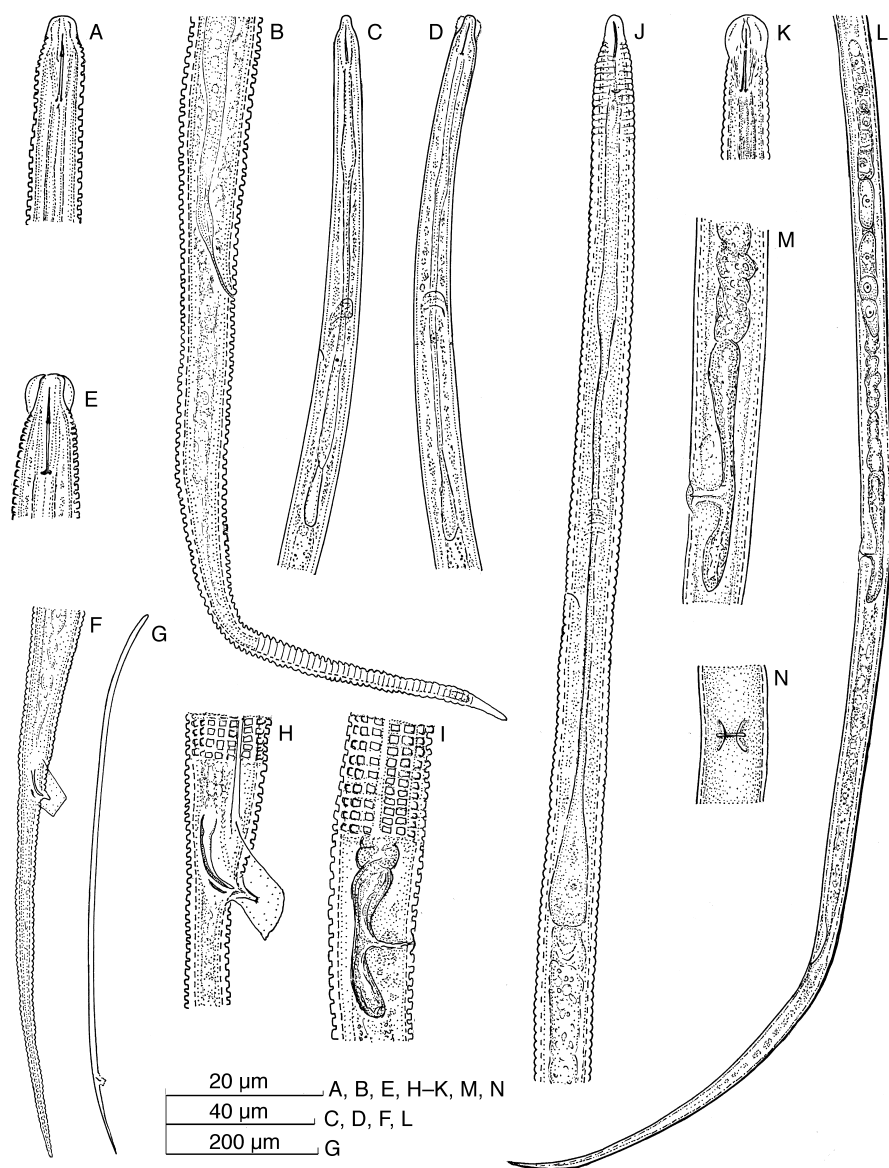
*Tenunemellus eurycephalus* (de Man, 1921) Siddiqi, 1986

syn. *Tylenchus eurycephalus* de Man, 1921

*Anguillulina eurycephalus* (de Man) Goodey, 1932

*Ditylenchus eurycephalus* (de Man) Filipjev, 1936

*Ecphyadophoroides eurycephalus* (de Man) Raski, Koshy & Sosamma, 1982



**Fig. 35.** A–I. *Ecphyadophoroides annulatus* Corbett. A–C, G and I. Holotype female. D, E, F and H. Paratype male. D and E. Ventral, remainder lateral views. A, C–E. Head ends. B and F. Tail ends. G. Entire male. H and I. Spicular and vulval regions, respectively. J–N. *Tenunemellus tenuis* (Corbett), holotype female. J. Oesophagus. K and N. Ventral, remainder lateral views. K. Head end. L. Posterior region of body. M and N. Vulval regions.

**ETYMOLOGY.** *Tenu* from prefix of type species name, Latin *tenuis* = thin, slender, and *nemella* = diminutive of nema.

The type species was found around roots of *Fimbristylis* sp. growing in waterlogged grassland near the Chirunde Compound road turn-off, Outer Circular Road, Zomba Mountain, Malawi.

**Genus *Lelenchus* Andrásy, 1954**

**syn. *Tylenchus* (*Lelenchus* Andrásy, 1954)**

(Fig. 36, A')

**Diagnosis**

Ecphyadophoroidinae. Body slender ( $a = 37\text{--}93$ ), under 0.75 mm long, almost straight when relaxed. Cuticle smooth or indistinctly striated, **lacking longitudinal ridges**. **Lateral field obscure or with two incisures delimiting single ridge**. **Cephalic region elevated, dorsoventrally flattened**, labial disc rounded, small; framework lightly sclerotized. **Amphidial apertures longitudinal clefts** running along most of lateral contour of cephalic region. Stylet delicate, with minute basal knobs, 7–11  $\mu\text{m}$  long. Orifice of dorsal gland close to stylet base. **Median oesophageal bulb oval, weakly muscular**. Basal bulb pyriform to saccate, enclosing glands. Vulva flush with body contour, with lateral membranes; lips not modified. Tail very long, filiform, with pointed terminus. Spicules tylenchoid, cephalated, ventrally arcuate. Gubernaculum present. **Bursa flaps simple, low, with convex margins**. Cloacal lips not forming a penial tube.

**Type species:**

*Lelenchus leptosoma* (de Man, 1880) Andrásy, 1954

syn. *Tylenchus leptosoma* de Man, 1880

*Tylenchus filiformis* var. *leptosoma* de Man, 1880 (Micoletzky, 1922)

*Anguillulina leptosoma* (de Man) Goodey, 1932

*Lelenchus leptosoma* (de Man) Meyl, 1961

*Filenchus leptosoma* (de Man) Andrásy, 1972

*Deontolaimus tatricus* Daday, 1896 (apud Andrásy, 1954)

**Other species**

*Lelenchus filicaudatus* Raski & Geraert, 1986 (original spelling *filicaudata*)

ETYMOLOGY. *Le* from prefix of type species name, and *lenchus* from *Tylenchus*.

The type species was found in moist soil of meadows and marshlands near Erlangen, Germany. The species is widely distributed. Raski & Geraert (1986) studied specimens of *L. leptosoma* from Alaska and Colorado, USA and from Chile and re-diagnosed the genus. They described *L. leptosoma* and *L. filicaudatus* from moist soil under thick tundra at Orange Bay, Hoste Island, Chile.

**Genus *Chilenchus* gen. n.**

(Fig. 36, B')

**Diagnosis**

Ecphyadophoroidinae. Body elongate and slender ( $L = 0.77\text{--}0.93$ ;  $a = 54\text{--}77$  in females of type species), slightly arcuate ventrally when relaxed. Cuticle indistinctly

striated, lacking longitudinal ridges. Lateral field with four incisures, showing two prominent ridges separated by a gap. Cephalic region elevated, dorso-ventrally flattened, labial disc rounded, small; framework lightly sclerotized. Amphidial apertures longitudinal sinuate clefts running along most of lateral contour of cephalic region. Stylet delicate, without basal knobs or thickenings, 10–13  $\mu\text{m}$  long in type species. Orifice of dorsal gland at stylet base. Median oesophageal bulb oval, poorly muscular. Isthmus elongate. Basal bulb saccate, enclosing glands, offset from intestine. Excretory pore at base of isthmus. Deirids not seen. Prophasms 24–30  $\mu\text{m}$  behind vulval level, on dorsal band of lateral field in type species. Vulva flush with body contour, with lateral membranes; lips not modified. Vagina straight, perpendicular to body axis. Postvulval uterine sac short. Spermatheca oval, offset. Ovary with oocytes in multiple rows. Tail very long, filiform, with pointed terminus. Spicules angular near middle, 12–15  $\mu\text{m}$  long in type species. Gubernaculum fixed, 3–4  $\mu\text{m}$  long in type species. Bursa simple, low, adanal, with convex margins. Cloacal lips not forming a penial tube.

#### Type species

*Chilenchus elegans* (Raski & Geraert, 1986) gen. n., comb. n.

syn. *Lelenchus elegans* Raski & Geraert, 1986

No other species.

#### Remarks

*Chilenchus* gen. n. comes close to *Lelenchus* and *Tenunemellus*, from which it differs in having lateral fields with two prominent ridges, oocytes in multiple rows, angular spicules and stylet lacking basal knobs. It has some affinities with *Filenchus*, particularly in spicule shape, but can be differentiated from it by the attenuated body, sinuate amphidial slits and knobless stylet.

ETYMOLOGY. *Chile* from country of its occurrence, and *enchus* from *Tylenchus*.

The type species was collected from moist soil under thick tundra at Orange Bay, Hardy Peninsula, Hoste Island, Chile.

### Genus *Mitranema* Siddiqi, 1986

(Figs 37; 38)

#### Diagnosis

Ecphyadophoroidinae. Body not abruptly narrowed behind vulva and cloacal lips. Annules distinct, formed by transverse grooves, margins zig-zag and wavy. Lateral field with a single ridge forming two incisures. Cephalic region continuous, striated, circular, with a prominent, offset labial disc. Amphidial apertures pore-like, on labial disc, obscure. Corpus cylindroid, with a basal swelling devoid of myofibrils and refractive thickenings. Isthmus long, slender. Basal bulb containing oesophageal glands. Cardia rounded. Vulva lacking lip flaps or lateral membranes; lips not modified. Prophasms dorso-sublateral, postmedian, a little anterior to vulva. Tail long, filiform, pointed. Spicules tylenchoid. Gubernaculum linear.

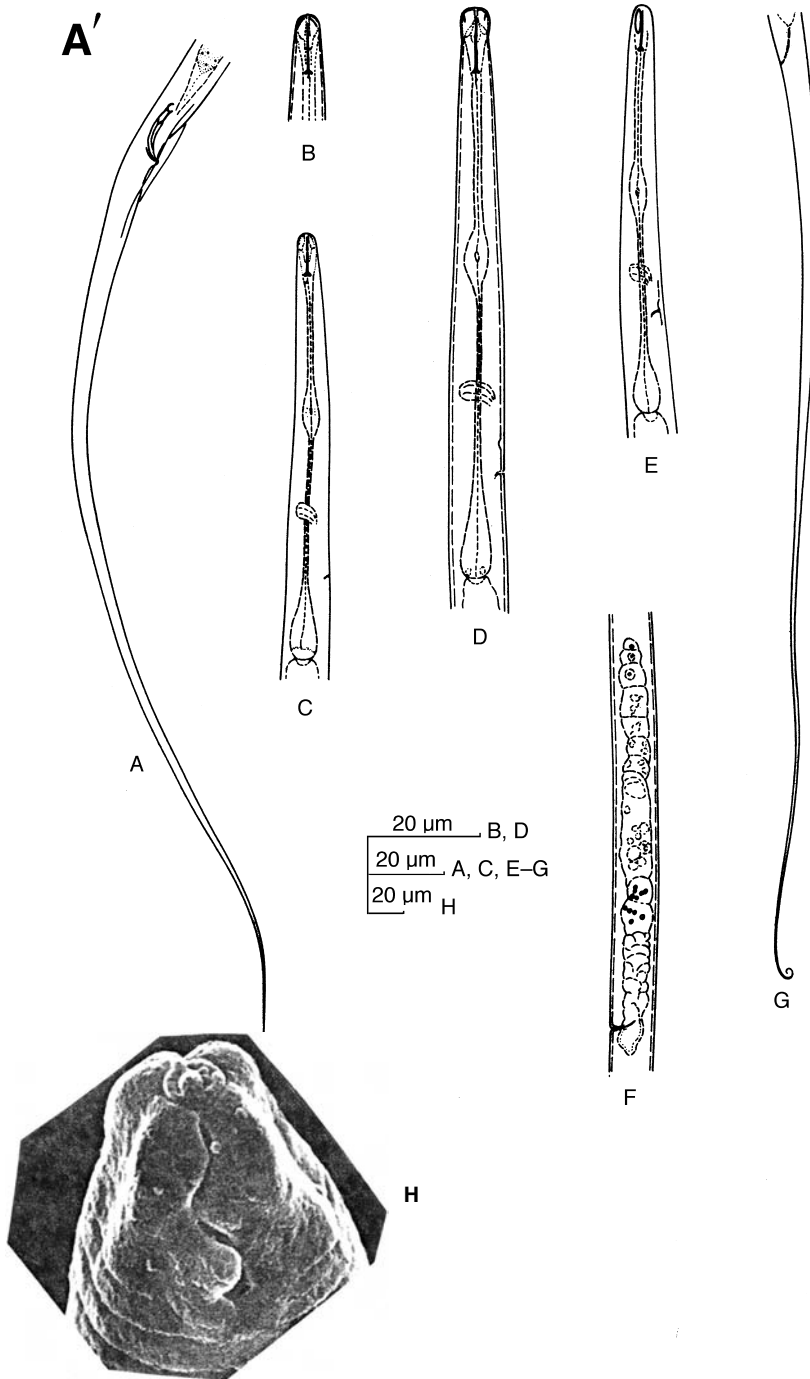
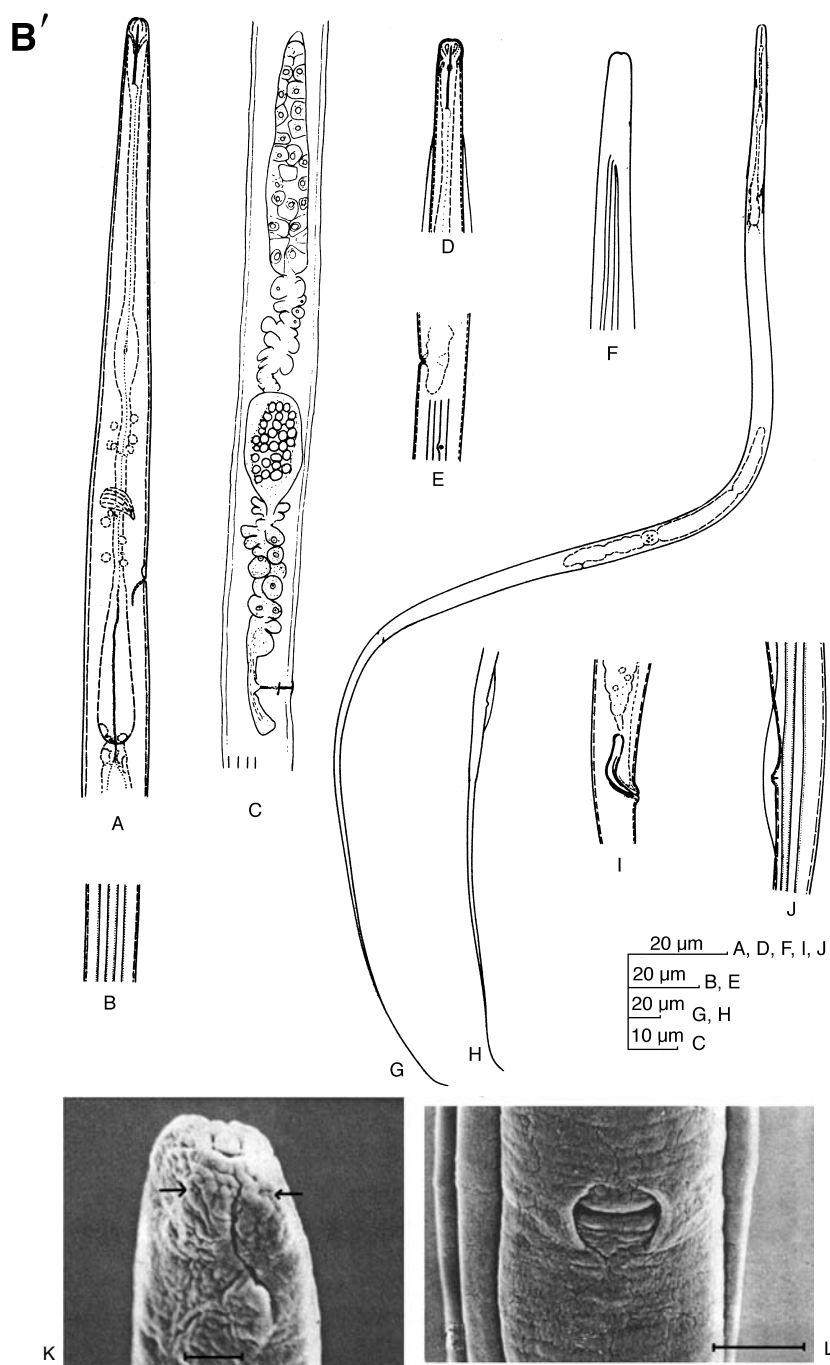
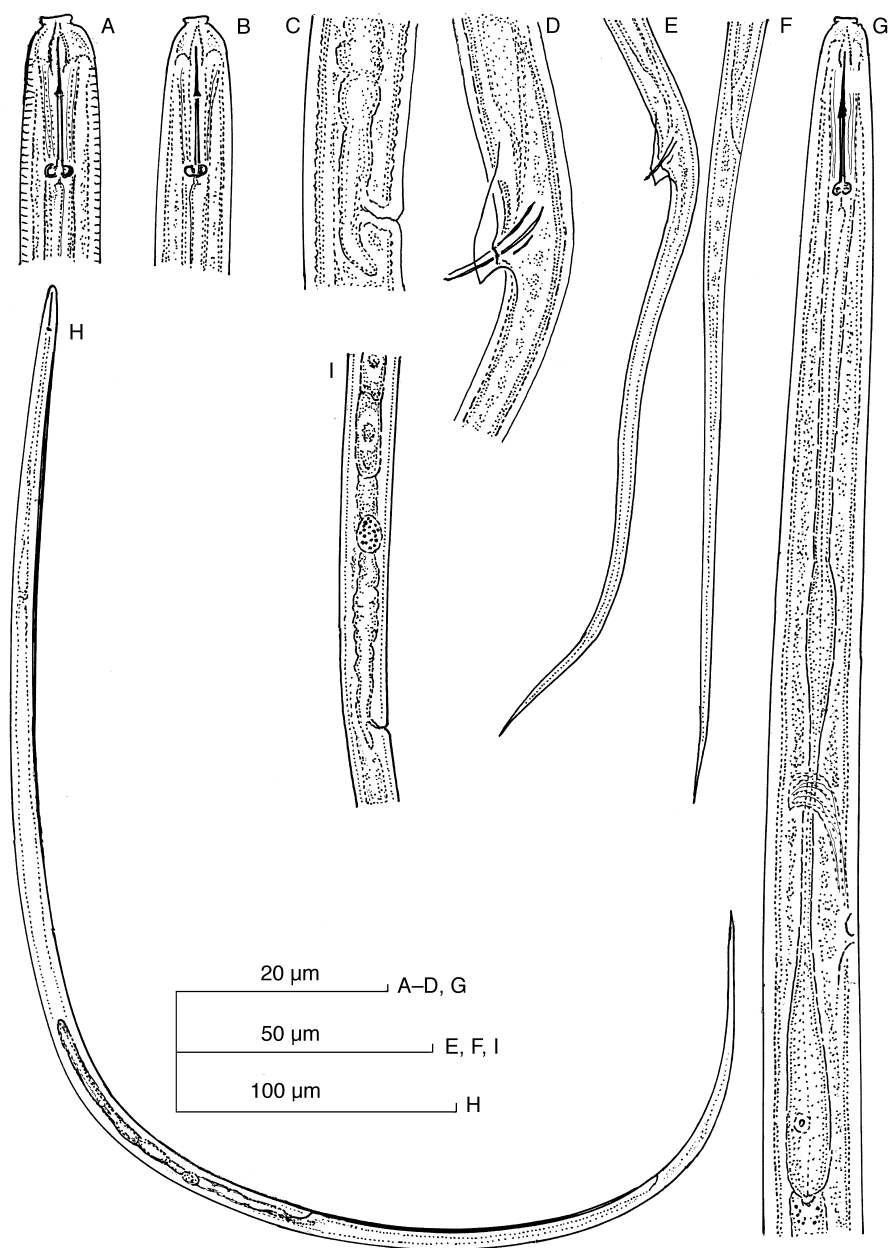


Fig. 36. A'. *Lelenchus leptosoma* (de Man). A, D, E. Males, remainder females. H. Scanning electron micrograph of head showing sinuate amphidial aperture. (A–G. After Geraert & Raski, 1986, courtesy *Nematologica*. H. After Brzeski & Sauer, 1983.)

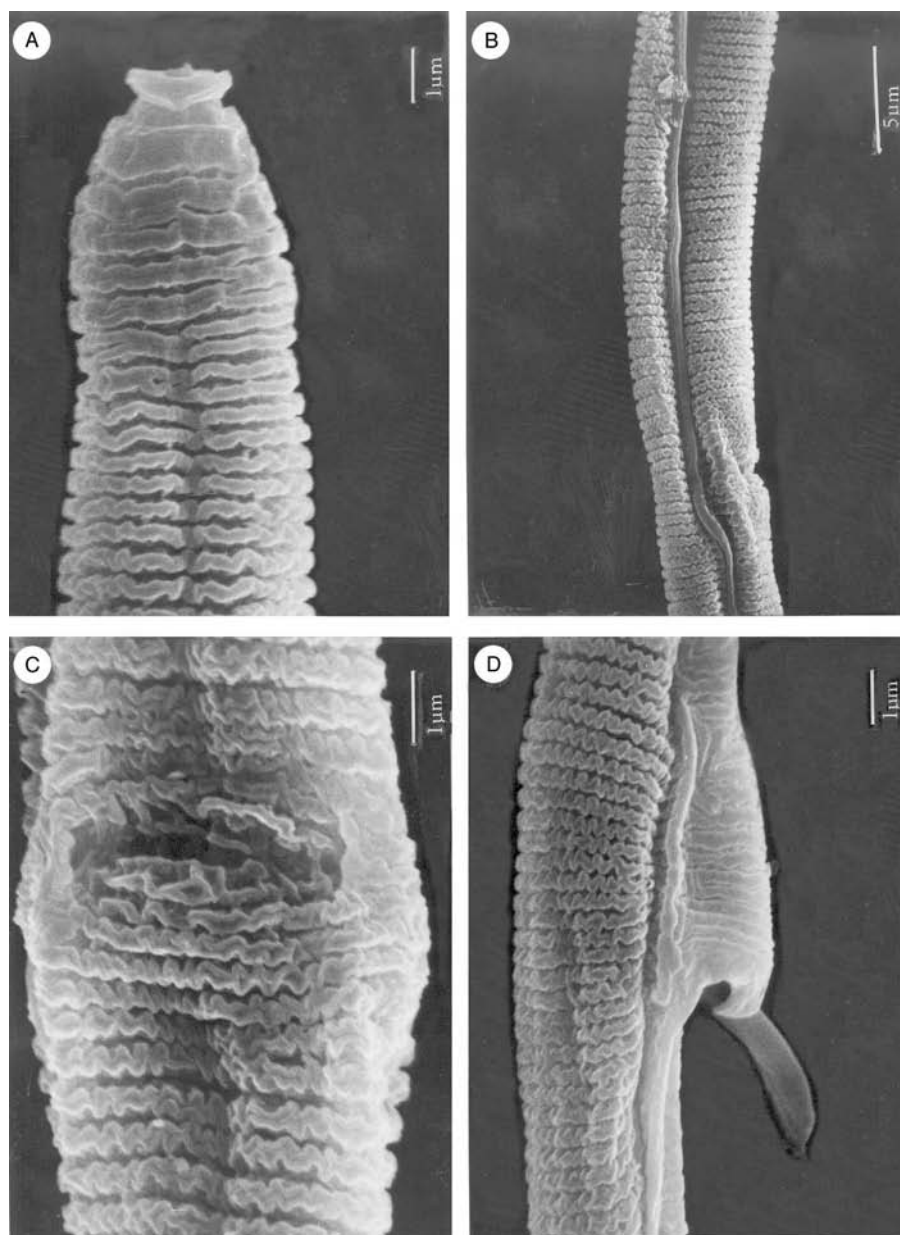




**Fig. 36. B'. *Chilenchus elegans*** (Raski & Geraert, 1986) gen. n., comb. n. A–G. Females. H–J. Males. Scanning electron micrographs: K. Head, lateral view showing sinuate amphidial aperture. L. Vulval region, ventral view showing lateral membranes and raised lateral field ridges. (After Geraert & Raski, 1986, courtesy *Nematologica*.)



**Fig. 37.** *Mitranema mitrum* Siddiqi, 1986. B, D and E. Males, remainder females. A and B. Head ends. C and D. Vulval and spicular regions, respectively. E and F. Tails. G. Oesophagus. H. Entire female. I. Genital branch.



**Fig. 38.** Scanning electron micrographs of *Mitranema mitrum* Siddiqi, 1986. A. Head end. B. Annules and lateral field in prevulval region. C. Vulval region in ventral view. D. Bursa region.

Margins of bursa flaps anteriorly convex, posteriorly concave, terminally lobed, directed backwards. Cloacal lips narrow, not forming a penial tube.

#### Type species

*Mitranema mitrum* Siddiqi, 1986

#### Other species

*Mitranema ornatum* Siddiqi, 1994

ETYMOLOGY. The neuter generic name is derived from Latin *mitra* = an Asiatic head-dress or turban, refers to the labial disc, and *nema* = nematode.

The type species was found in forest soil at 25 miles east of Ore on the Ore–Benin City Road, Nigeria. *Mitranema ornatum* was also found in forest soil near Benin in Nigeria.

### Genus *Tremonema* Siddiqi, 1994

(Fig. 42, A–G)

#### Diagnosis

Ephyadophoroidinae. Body about 0.5 mm long, slender ( $a > 50$ ), ventrally arcuate upon relaxation. **Cuticle strongly and deeply annulated so that annules become angular and look like a wire spring in lateral view. Lateral field absent.** Deirids and prothasms not seen. Cephalic region conoid-rounded, continuous; lateral lip areas elevated, with pore-like amphids located near oral opening; perioral disc and papillae indistinct; framework not sclerotized. Stylet thin, under 10  $\mu\text{m}$  long; conus less than half stylet length; knobs tiny. Orifice of dorsal oesophageal gland at base of stylet. **Oesophagus tylenchoid with median and basal bulbs.** Precorpus and isthmus elongate-slender. Median bulb lacking musculature and refractive thickenings. Excretory pore located near base of isthmus in type species. Cardia rounded. Vulva a transverse slit in a depression of body, facing backward, at 65% of body in type species; lateral membranes absent. **Vagina straight, leading inward and forward,** its walls not sclerotized. Ovary anteriorly outstretched. Spermatheca round, with small rounded perm. **Postvulval uterine sac absent. Tails elongate-conoid to a pointed terminus, straight.** Male head, stylet and oesophagus as described for female. **Bursa narrow, lobe-like with narrow tip, projecting outward and backward.** Spicules cephalated, pointed, strongly arcuate ventrally, 10  $\mu\text{m}$  long in type species. Gubernaculum small, fixed.

#### Type species

*Tremonema tremulum* Siddiqi, 1994

No other species.

ETYMOLOGY. Generic name is derived from Greek, *tremo* = quivering, and *nema* = nematode and refers to the deeply annulated cuticle giving the body great elasticity.

The type species was found in soil around roots of a forest tree, *Mitragyna ciliata* in Korup National Park, Ndian Division, South-West Province, Cameroon.

## FAMILY ATYLENCHIDAE

### (Tylenchoidea with cephalic setae)

The family comprises two somewhat unusual and taxonomically very interesting genera, *Atylenchus* and *Eutylenchus*, which are unique among the entire order in having four cephalic setae. Perhaps too much phylogenetic importance was attached to this character by Golden (1971), who elevated this family to superfamily rank and remarked that they 'possibly represent a link between tylenchs and dorylaims' connecting to *Encholaimus* (Dorylaimida), which has cephalic setae and a similar cuticular pattern. Siddiqi (1983) considered these characters of *Encholaimus* as specialized adaptations and Andr  ssy (1976) classified atylenchs with *Pleurotylenchus*, a genus with a similar cuticle pattern but lacking cephalic setae. The four cephalic papillae in Tylenchoidea are generally present on the surface and in atylenchs they 'shoot out', maybe as a manifestation of an ancestral latent character. The subfamily Eutylenchinae, otherwise, is closely related to Tylodoridae and this is supported by the character of the stylet being about as long as the precorpus (cf. *Cephalenchus*).

On the basis of the synapomorphy of cephalic setae, Atylenchidae stands out within the Tylenchata. However, using SEM of cephalic structures, *Atylenchus* shows an undivided oral or labial plate with the amphidial apertures appearing as longitudinally oval slits and confined to this plate. *Eutylenchus*, on the other hand, has longitudinal slit-like amphidial apertures slightly extending laterally but remaining within the frontal region of the head. On the basis of cephalic structures, Geraert & Raski (1987) grouped *Atylenchus* with *Aglenchus*, *Coslenchus* and *Antarctenchus*, while *Eutylenchus* formed a group with *Cephalenchus*, *Tyldorus* and *Campbellenchus*. The two genera of Atylenchidae are far removed from each other and therefore Siddiqi's (1986) classification keeps them in separate monotypic subfamilies.

Tylenchoidea are very heterogeneous in the structures of the cephalic region (i.e. labial plate/disc, amphids, sensilla) and therefore classification based entirely on these structures will produce different groupings of genera from those proposed here.

*Atylenchus decalineatus* was found in a cranberry bog in New Jersey (USA) and later in other places in the USA and Germany. *Eutylenchus setiferus* and *E. vitiensis* occur in Australia and the Fiji Islands, respectively, and *E. africanus* in Africa and India.

## Family Atylenchidae Skarbilovich, 1959

### Diagnosis

Tylenchoidea. Slender nematodes, about 1 mm or less long. **Four cephalic setae present**, a unique character in Tylenchida. No marked sexual dimorphism in anterior region except in shape of cephalic setae. **Body with longitudinal ridges all around**; annulations formed by transverse grooves crossing longitudinal ridges except laterally and dividing the surface into minute blocks. Lateral fields with one to three ridges. Cephalic region small, continuous or set off, annulated or smooth, **with cephalic setae**. **Stylet moderately developed, slender, about as long as precorpus**. **Median bulb muscular**, with distinct refractive thickenings. Basal bulb enclosing glands; cardia present. Vulva transverse, in posterior region. Vagina directed inward. Postvulval uterine sac present. Ovary single, anteriorly

outstretched. Testis single, outstretched; sperm small, round. Tails in both sexes long, filiform. Prothasms, where known, dorso-sublateral, postmedian, near to vulva. Bursa absent in type genus, in other genus conspicuous, adanal, lobed. Spicules tylenchoid, cephalated, arcuate, pointed. Gubernaculum simple, fixed. Cloacal lips not forming a penial tube.

#### Type subfamily

*Atylenchinae* Skarbilovich, 1959

#### Other subfamily

*Eutylenchinae* Siddiqi, 1986

### Key to subfamilies of *Atylenchidae*

1. Lateral field with two or more ridges, cephalic region broad, annulated, continuous, bursa absent ..... ***Atylenchinae***  
 Lateral field with one ridge, cephalic region narrow, smooth, offset, bursa present ..... ***Eutylenchinae***

### Subfamily *Atylenchinae* Skarbilovich, 1959

#### Diagnosis

*Atylenchidae*. Small nematodes (0.5–0.8 mm), with four cephalic setae. Body annulated by transverse grooves, or striae, interrupted by lateral ridges. Longitudinal ridges around body for most of its length present, **two or more elevated lateral ridges representing lateral fields** (in juveniles laterals are bifid forming three incisures) and four longitudinal ridges each in dorsal and ventral sectors in type genus; **no ridges in middorsal or midventral line. Deirids present. Cephalic region broad, continuous, slightly flattened dorso-ventrally, annulated. Stylet about as long as precorpus**, with well-developed knobs. Vulva lacking lateral membranes. Postvulval uterine sac present. **Bursa absent**, male tail not abruptly narrowed behind cloacal lips which are slightly raised.

#### Type genus

*Atylenchus* Cobb, 1913

No other genus.

### Genus *Atylenchus* Cobb, 1913

(Fig. 39)

#### Diagnosis

*Atylenchinae*, with characters of the subfamily. **Body slightly flattened dorso-ventrally**. Annules prominent. Cephalic region with four to five annules; setae tapering to fine points, 6–9  $\mu\text{m}$  long. Stylet 17–19  $\mu\text{m}$  or as long as precorpus in female, 17  $\mu\text{m}$  long in male, conus slightly shorter than shaft, knobs rounded. Excretory pore near base of isthmus. Deirids just above level of excretory pore. Median bulb with prominent refractive thickenings. Nerve ring crossing isthmus near middle. Basal bulb a little more than body width long, base offset from intestine. **Vulva lack-**

**ing lateral membranes**, lips not modified. Postvulval uterine sac about one body width long. Testis single, outstretched. **Bursa absent**. Spicules tylenchoid, about 20  $\mu\text{m}$  long. Gubernaculum fixed.

#### Type species

*Atylenchus decalineatus* Cobb, 1913

syn. *Eutylenchus decalineatus* (Cobb) Micoletzky, 1922

No other species.

ETYMOLOGY. Greek *a* = without, and *Tylenchus* (= *Tylenchus* lacking a bursa).

*Atylenchus decalineatus* was found on roots of cranberries in a cranberry bog, New Lisbon, New Jersey; Atwood Grove, Florida, USA.

### Subfamily Eutylenchinae Siddiqi, 1986

#### Diagnosis

Atylenchidae. Small to medium-sized nematodes (0.56–1 mm), **with cephalic setae**; male cephalic setae shorter than those of female. Annules formed by **transverse grooves or striae not interrupted by lateral fields**. Longitudinal ridges around body include **lateral ridges not different from others** and mid-dorsal and mid-ventral ridges. Amphid apertures indistinct, labial. **Deirids reduced or absent**. **Cephalic region small, narrow, offset**, not annulated in type genus. Stylet slender, about as long as precorpus, with distinct basal knobs. Median oesophageal bulb oval, muscular, with large refractive thickenings in centre. Basal bulb large, saccate. **Vulva with lateral cuticular membranes**; lips not modified. Postvulval uterine sac present. Ovary single, anteriorly outstretched. Tails elongate-conoid to filiform. **Bursa lobed**, posteriorly directed. Cloacal lips raised but not forming a tube; body behind them abruptly narrowed.

#### Type genus

*Eutylenchus* Cobb, 1913

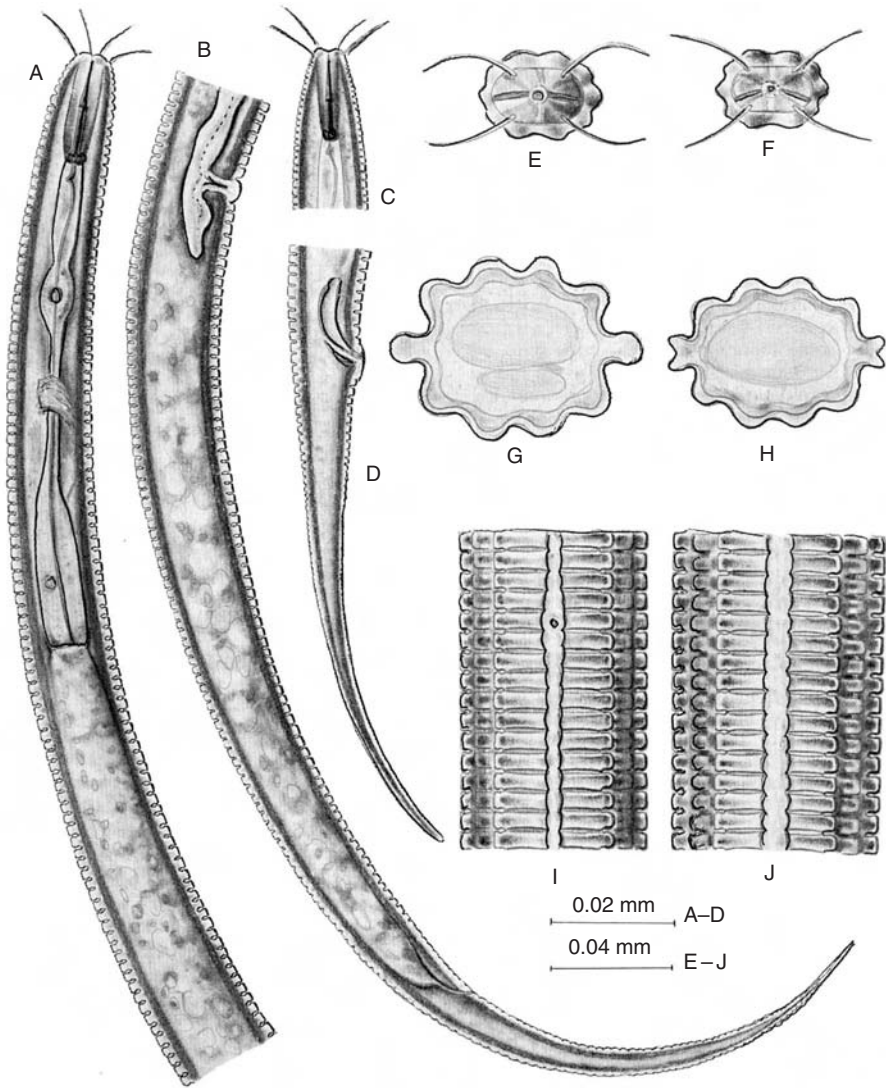
No other genus.

#### Genus *Eutylenchus* Cobb, 1913

(Figs 8(a)D; 8(c)A; 40)

#### Diagnosis

Eutylenchinae, with characters of the subfamily. Body arcuate upon relaxation. **Annules coarse, formed by transverse grooves**. **Cuticle bearing 12 similar longitudinal ridges on most of body, divided into blocks by transverse grooves**. Cephalic region four-lobed, offset, each lobe with a cephalic seta; framework lightly sclerotized, labial disc indistinct. Female cephalic setae 9–12  $\mu\text{m}$  long, finely drawn out terminally, with inward-pointing projection near base; those of male shorter and rod-like. Stylet 18–32  $\mu\text{m}$  long, conus solid-appearing anteriorly, shorter than shaft, basal knobs rounded. Orifice of dorsal gland close behind base of stylet. Excretory pore in region of isthmus, median bulb oval, with prominent refractive thickenings.



**Fig. 39.** *Atylenchus decalineatus* Cobb. A and B. Anterior and posterior regions of female, respectively. C and D. Head end and tail end of male, respectively. E and F. *En face* views of female and juvenile respectively. G and H. Cross-section of body of female and juvenile, respectively. I and J. Surface views of female near deirid and midbody, respectively. (After Sher *et al.* (1966), courtesy Helminthological Society of Washington.)

Basal bulb elongate-saccate. Cardia rounded. **Vulva distinct but small, with cuticular lateral membranes.** Postvulval uterine sac about one body width long. Spermatheca axial, oval to elongate, may contain large sperm. Crustaformeria tricollellate, each column with seven to eight cells. Ovary with single row of over 15



oocytes. Tail regularly tapering to a fine tip, over ten anal body widths long. **Bursa lobed**, with crenate margins. Spicules well developed, 15–18  $\mu\text{m}$  long in type species. Gubernaculum about half the size of spicule fixed.

#### Type species

*Eutylenchus setiferus* (Cobb, 1893) Cobb, 1913  
syn. *Tylenchus setiferus* Cobb, 1893

#### Other species

*Eutylenchus africanus* Sher, Corbett & Colbran, 1966  
syn. *Eutylenchus orientalis* Husain & Khan, 1968  
*E. excretorius* Ebsary & Eveleigh, 1981  
*E. fueguensis* Valenzuela-A. & Raski, 1985  
*E. vitiensis* Orton Williams, 1979

ETYMOLOGY. Greek prefix *eu* = good, and *Tylenchus*.

The type species was found in plant soil from hills opposite Harwood, Clarence River, northern New South Wales, Australia. A key to the species of *Eutylenchus* is given by Brzeski (1996).

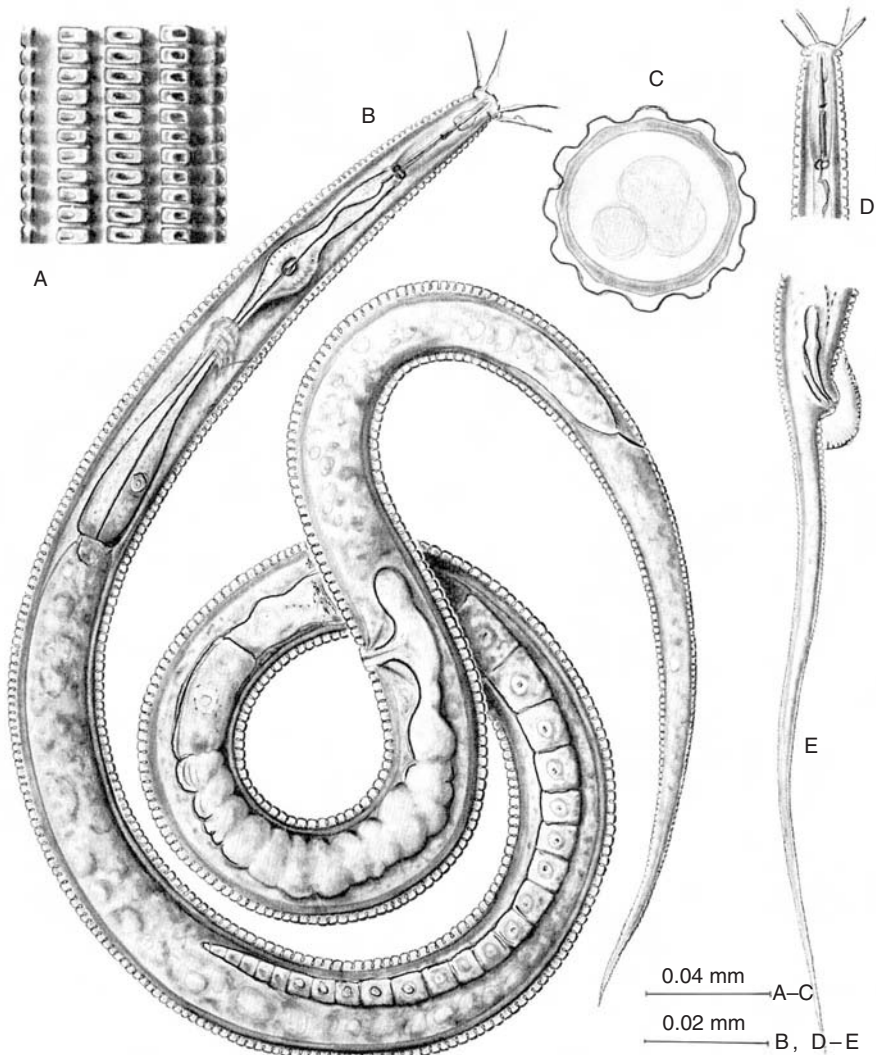
## FAMILY TYLODORIDAE

### (Tylenchoidea with a strong stylet and elongate axial spermatheca)

Tylodoridae belongs to the superfamily Tylenchoidea because its members have sub-median, dorso-sublateral prothasms (phasmid-like structures) outside the lateral fields and lack phasmids, but differs from the Tylenchidae and Ecphyadophoridae in having a strong stylet measuring about as long as or longer than the precorpus, reaching up to 100  $\mu\text{m}$ , and an elongate axial spermatheca. The long stylet-bearing *Tylodorus* and *Arboritynchus* give the impression that they are close relatives of *Dolichodorus*, *Macrotrophurus* and *Belonolaimus* of the Dolichodoridae, but the latter genera, however, are didelphic and have distinct phasmids in the tail region and belong to Hoplolaimina.

With their long stylet and powerful median oesophageal bulb, Tylodoridae are capable of feeding on roots of higher plants. Khera & Zuckerman (1963) reported that *Cephalenchus* sp. (called *Tylenchus agricola*) fed on root epidermal cells of cabbage and cauliflower. *Cephalenchus emarginatus* reproduced well on maple and several conifer seedlings and in callus cultures; its feeding caused root stunting, but necrosis was not observed (Gowen, 1970). On *Picea sitchensis*, the nematodes reproduced by parthenogenesis and the life cycle was completed in 5–6 days at 25°C and in 13–15 days at 15°C; no reproduction occurred at 30°C or below 10°C (Gowen, 1970). *Cephalenchus* spp. have a worldwide distribution but, since they do not cause severe damage, they are not considered as important plant parasites.

*Tylodorus fisheri* was observed to feed on root tips of *Eucalyptus* for 2–4 h. The long stylet was thrust deep into root tissues and successful feeding took place when



**Fig. 40.** *Eutylenchus setiferus* Cobb. A and C. Surface view and cross-section of female body, respectively. B. Entire female. D and E. Anterior and posterior ends of male, respectively. (After Sher *et al.* (1966), courtesy Helminthological Society of Washington.)

the median bulb was seen to be regularly pulsating. The nematode fed on the roots of *Eucalyptus regnans* and *E. obliqua* (Reay, 1991).

Meagher (1964) found it attractive to postulate that *Tylodorus* and *Dolichodorus* had a common ancestor and that the latter genus had evolved from a filiform-tailed ancestor. Loof (1958) had argued for the placement of *Dolichodorus* in the Tylenchinae and *Belonolaimus* in the Hoplolaiminae. *Tylodorus*, *Cephalenchus* and *Epicharinema* are monodelphic and lack phasmids, thus belonging to the infraorder

Tylenchata, while *Dolichodorus* is a member of Hoplolaimina. This removes the confusion which exists in the classification of these genera. Similarly, the confusion caused by assigning *Psilenchus* and *Atetylenchus* to Boleodorinae by Geraert & Raski (1987) can be removed by considering these genera as members of Hoplolaimina on the basis of their didelphy and presence of distinct phasmids in the tail region.

*Epicharinema keralense* was found around roots of coconut in Kerala State, India. Its systematic position in Ecphyadophorinae as suggested by Raski *et al.* (1980) has been questioned by Siddiqi (1986) on the grounds that it has a strong stylet and median oesophageal bulb and no postvulval uterine sac. Obviously, *Epicharinema* does not fit well with *Ecphyadophora* and *Ecphyadophoroides*, although it has a similar attenuated body and lobed bursa. It is a close relative of *Gracilancea* Siddiqi, 1976 and is placed with it in a separate subfamily, Epicharinematinae.

*Pleurotylenchus* Szczygieł, 1969 and *Campbellenchus* Wouts, 1978 have been assigned to separate monotypic subfamilies, namely, Pleurotylenchinae and Campbellenchinae, respectively. Andrásy (1976) assigned Pleurotylenchinae to the family Atylenchidae, while Wouts (1978) placed Campbellenchinae in Tyldoridae *sensu* Siddiqi (1976). Wouts (1978) differentiated Campbellenchinae from Tyldoridae by the structure of its cuticle, shorter stylet and the lack of a labial disc. The cuticle having longitudinal grooves but no transverse grooves or striae behind the stylet region in *Campbellenchus* is considered here as a functional adaptation. The genus shares many similarities (including position of the prophasmids (see Siddiqi, 1978)) with *Cephalenchus* and should be placed with it in the subfamily Pleurotylenchinae.

Tyldoridae represents the most evolved plant-parasitic Tylenchata. No doubt, it is a heterogeneous group with members coming from more than one ancestor. But the apomorphy of advanced plant parasitism shown by them coupled with synapomorphies of long and strong stylet, elongate axial spermatheca and heavy build of spicules (cf. *Tyldorus*, *Cephalenchus*, etc.) help in uniting them in one family. The diversity of the tyldorid genera, however, demands grouping on various morphological characters. This is the reason to recognize three subfamilies – Tyldoridae, Pleurotylenchinae and Epicharinematinae.

As regards the placement of *Pleurotylenchus* with the atylenchs as suggested by Andrásy (1976) and supported by Raski *et al.* (1980) and Geraert & Raski (1987), I would agree with Wouts (1978) that the cephalic setae, and not the longitudinal cuticular grooves or striae, should be considered diagnostic for the Atylenchidae; *Pleurotylenchus* is a relative of *Cephalenchus* and *Campbellenchus* and is here assigned along with them to the subfamily Pleurotylenchinae.

## Family Tyldoridae Paramonov, 1967 (Siddiqi, 1976)

### Diagnosis

Tylenchoidea. Medium to large (0.6–2 mm), slender; cuticle prominently annulated or smooth. Lateral field with four or six incisures at midbody, rarely obscure. Cephalic region usually small, continuous or offset by constriction; **cephalic setae absent**; a conspicuous labial disc present in Tyldoridae. Amphidial apertures longitudinal slits near labial plate/disc or cleft-like extending along the lateral side of cephalic region. Deirids present. Prophasmids dorso-sublateral, postmedian. Stylet well developed,

about as long as precorpus or longer, reaching a length of about 100  $\mu\text{m}$ ; conus equal to or longer than the shaft; basal knobs prominent. Protractor muscles tubular around stylet. Orifice of dorsal oesophageal gland at base of stylet. **Precorpus as long as or shorter than stylet. Median oesophageal bulb well developed**, with prominent refractive cuticular thickenings. Isthmus slender, longer than precorpus. Oesophageal glands enclosed in basal bulb or rarely dorsal gland may extend slightly over intestine. Vulva with or without lateral membranes. Postvulval uterine sac present, prominent or absent (Epicharinematinae). Vagina directed inward or forward. **Spermatheca large axial, oblong to more elongate**. Ovary outstretched. Crustaformeria usually a quadricolumella with five to six cells in each row. **Tails in females, males and juveniles elongate-filiform. Cloacal lips not tubular**. Testis outstretched. Sperm small to medium-sized. Bursa adanal, simple or lobed. Spicules moderately robust. Gubernaculum linear, fixed. Deep root feeders.

#### Type subfamily

Tylodorinae Paramonov, 1967

#### Other subfamilies

Epicharinematinae Maqbool & Shahina, 1985

Pleurotylenchinae Andr  ssy, 1976

#### Key to subfamilies of Tylodoridae

1. Stylet over 75  $\mu\text{m}$  long; labial disc conspicuous; spicules of heavy build, robust ..... **Tylodorinae**  
 Stylet under 35  $\mu\text{m}$  long; labial disc inconspicuous; spicules not of heavy build ..... 2
2. Cuticle thick, strongly annulated, with or without longitudinal ridges; postvulval uterine sac prominent; bursa simple ..... **Pleurotylenchinae**  
 Cuticle thin, not strongly annulated; postvulval uterine sac absent; bursa lobed ..... **Epicharinematinae**

#### Subfamily Tylodorinae Paramonov, 1967

##### Diagnosis

Tylodoridae. Cuticle thick, with or without longitudinal ridges outside lateral fields. Lateral fields each with six incisures, often areolated. Cephalic region continuous or offset, four-lobed; **labial disc prominent**, round, offset. Amphidial apertures longitudinal slits at base of labial disc occupying only the front of the cephalic region. **Stylet over 75  $\mu\text{m}$  long. Precorpus short, its lumen convoluted**. Median bulb well developed. Basal bulb offset from intestine. Crustaformeria a quadricolumella with five to six cells in each row. **Spicules 30–50  $\mu\text{m}$  long, robust**. Bursa large, adanal, simple. Tails elongate, finely pointed, similar between sexes.

##### Type genus:

*Tylodorus* Meagher, 1964

## Other genera

*Arboritynchus* Reay, 1991

**Key to genera of Tylodorinae**

1. Cephalic region continuous, not lobed; lateral field beginning near middle of oesophagus ..... *Tylodorus*
- Cephalic region offset, with four prominent lobes; lateral field beginning at base of cephalic region ..... *Arboritynchus*

**Genus *Tylodorus* Meagher, 1964**

(Figs 8(d)C; 41)

## Diagnosis

Tylodorinae. Body long (1.3–1.9 mm) in type species. **Lateral field with six incisures**, irregularly areolated. Deirids present at level of excretory pore located opposite basal bulb. **Cephalic region continuous, with a distinct labial disc** and four lip areas each with a cephalic papilla; amphidial apertures longitudinal slits at base of labial disc. Stylet 76–104  $\mu\text{m}$  long in type species with conus longer than the shaft, knobs rounded, well separated from shaft. Orifice of dorsal oesophageal gland about 4  $\mu\text{m}$  behind stylet base. Precorpus short, broad, with convoluted lumen. Median bulb very muscular, with refractive thickenings, posterior to middle of oesophagus. Basal bulb saccate, offset from intestine. Ovary outstretched, with a single row of oocytes. Vulval lips not raised or modified; **lateral vulval membranes absent**. A postvulval uterine sac present. **Spermatheca oblong, axial**. Tail elongate-tapering, with acuminate tip. **Spicules moderately robust, with dorsal flanges meeting medially**. Gubernaculum fixed. Bursa large, adanal. Cloacal lips slightly protruding; hypopygium absent.

## Type species

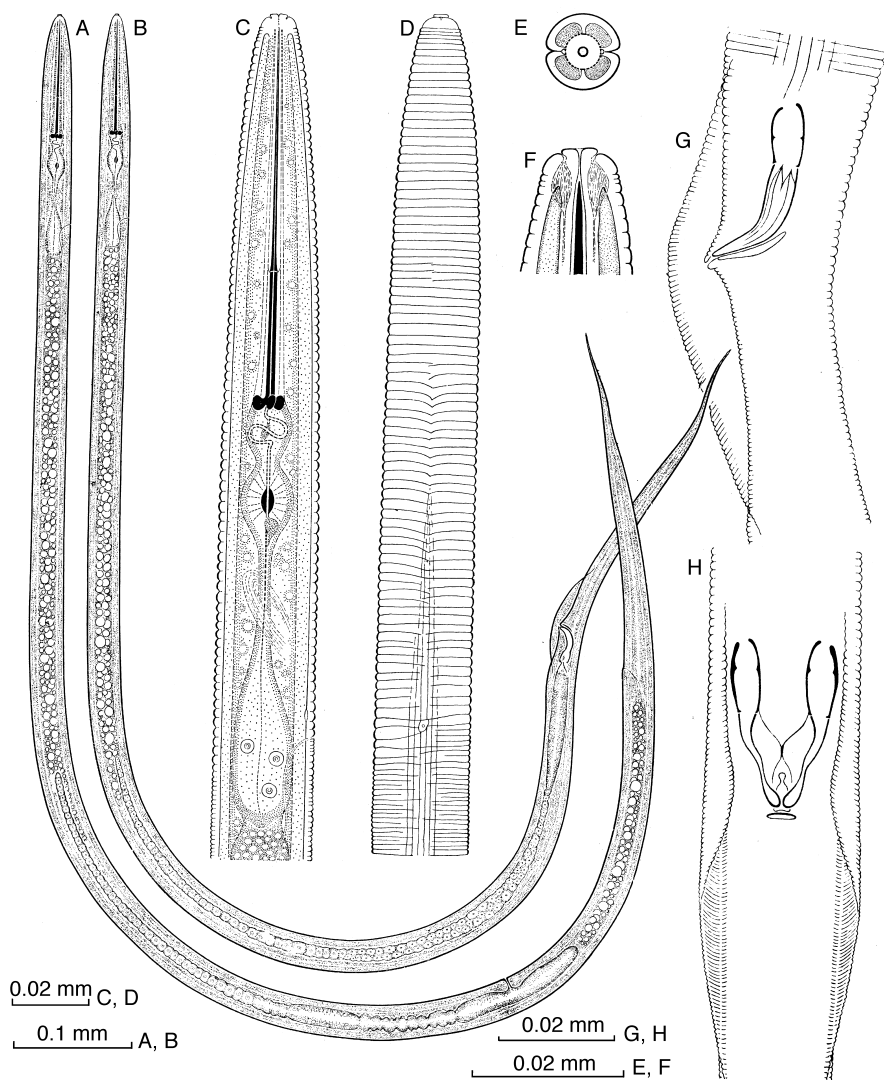
*Tylodorus acuminatus* Meagher, 1964

## Other species

*Tylodorus fisheri* Reay, 1991

ETYMOLOGY. From Greek *tylos* = knob, and *dory* = spear (the name was coined to indicate the immediate position of *Tylodorus* between *Tylenchus* and *Dolichodorus*).

The type species was found in virgin forest around the roots of *Eucalyptus* sp. at 2 miles along Coombs Road from the highway, Kinglake West, Victoria, Australia. *Tylodorus fisheri* was collected from *Eucalyptus ovata* forest in South Australia. The genus is confined to the Australian region.



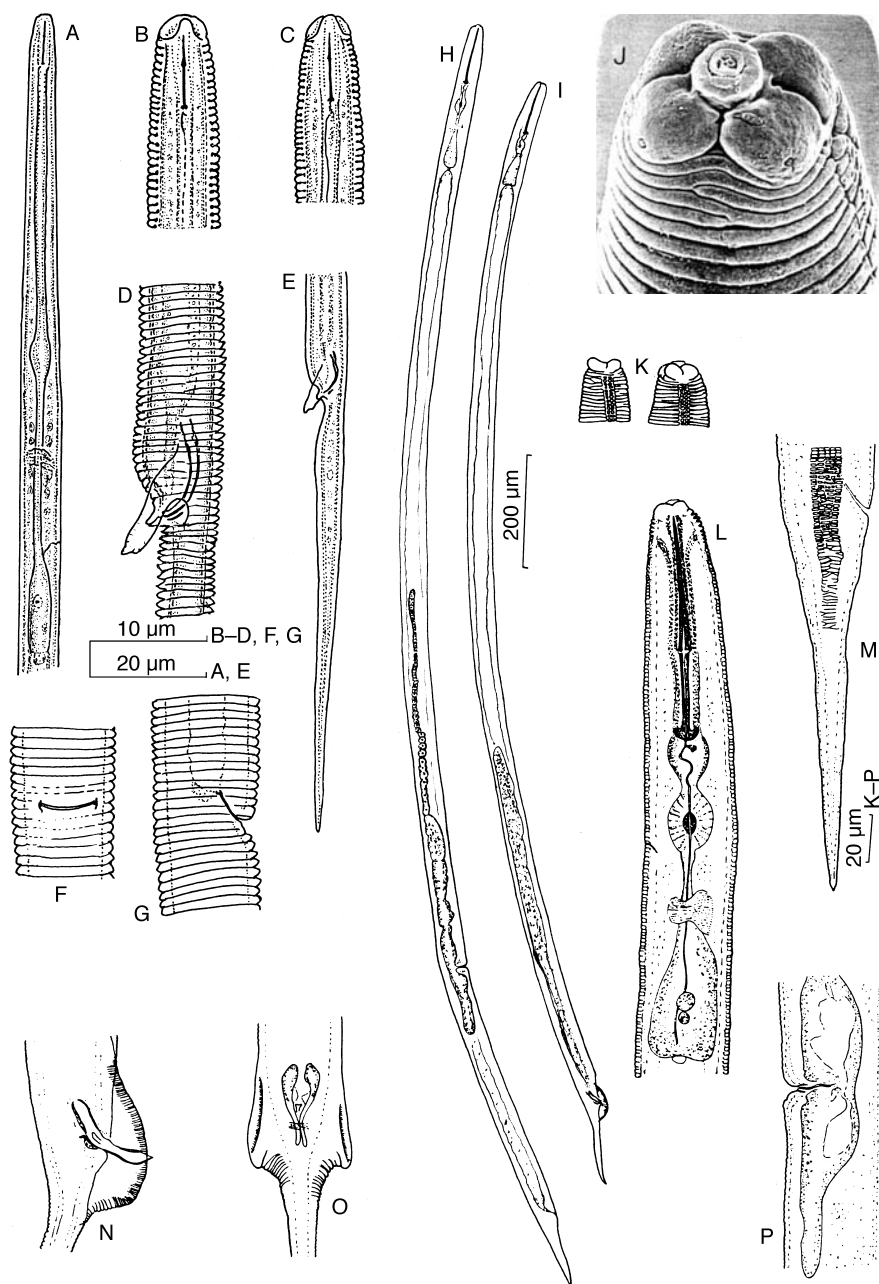
**Fig. 41.** *Tylodorus acuminatus* Meagher. A. Female. B. Male. C. Oesophageal region of female. D. Cuticular annules and lateral field in anterior region of female. E. *En face* view. F. Dorsoventral view of head. G and H. Bursa regions in lateral and ventral view, respectively. (After Meagher (1964), courtesy *Nematologica*.)

### **Genus *Arboritynchus* Reay, 1991**

(Fig. 42, H–P)

#### **Diagnosis**

Tylodorinae. Body 1.7–2.3 mm long, slender. **Cephalic region offset, with four pronounced lobes; labial disc distinct, rounded, offset, in SEM appearing double.** Amphidial apertures longitudinal slit-like at base of labial disc. Lateral field with six



**Fig. 42.** A–G. *Tremonema tremulum* Siddiqi. H–P. *Arboritynchus simpsoni* Reay. A, B, F, G, H, J–M and P. Females, remainder males. A and L. Oesophageal regions. B, C, J, K. Head ends. D, N, O. Spicular regions. E and M. Tail ends. F, G and P. Vulval regions. H and I. Adults. (A–G. After Siddiqi (1994), courtesy *Afro-Asian Journal of Nematology*. H–P. After Reay (1991).)

incisures, **beginning at the base of the cephalic region**. Deirids distinct. Prophasms not seen. **Stylet long (89–103  $\mu\text{m}$  in type species)**, robust; conus longer than shaft; knobs large, rounded. Median oesophageal bulb very muscular, offset from bulbous precorpus. Basal bulb large, saccate. Excretory pore opposite median bulb to a little behind nerve ring. Vulva at 70–75% of body in type species. Postvulval uterine sac about 1.5 times body width long. Crustaformeria with 20–24 cells in four rows. **Spermatheca elongate oval, axial**. Tail long (96–168  $\mu\text{m}$  in type species), acuminate. **Spicules robust, 45–51  $\mu\text{m}$  long in type species**, arcuate, cephalated. Gubernaculum curved, 7–12  $\mu\text{m}$  long in type species. Bursa large, adanal, with posterior margins slightly concave.

#### Type species

*Arboritynchus simpsoni* Reay, 1991

No other species.

ETYMOLOGY. From the Latin, *arborius* = pertaining to tree, and *tynchus* = contraction of *Tylenchus*.

The type species was found in tree soil in Mt Boss State Forest, north-west of Wauchope, New South Wales, Australia.

### Subfamily Pleurotylenchinae Andr ssy, 1976 syn. Campbellenchinae Wouts, 1978

#### Diagnosis

Tylodoridae. Cuticle thick, with or without longitudinal ridges outside lateral fields. Lateral fields each with four to six incisures. Cephalic region continuous or offset; **labial disc indistinct. Stylet about as long as precorpus, under 35  $\mu\text{m}$  long**. Median bulb well developed. Basal bulb offset, its dorsal gland occasionally forming a short lobe over the intestine. Spicules slender, ventrally arcuate. Gubernaculum linear. Bursa adanal, simple or lobed.

#### Type genus

*Pleurotylenchus* Szczygie , 1969

#### Other genera

*Campbellenchus* Wouts, 1978

*Cephalenchus* Goodey, 1962

#### Key to genera of Pleurotylenchinae

1. Longitudinal ridges outside lateral fields present; lateral vulval flaps absent ..... 2  
Longitudinal ridges outside lateral fields absent; lateral vulval flaps present ..... *Cephalenchus*
2. Body annulated behind stylet region; anterior vulval lip flap-like; bursa indistinct ..... *Pleurotylenchus*



Body not annulated behind stylet region; anterior vulval lip not flap-like;  
 bursa large, distinct ..... *Campbellenchus*

### Genus *Pleurotylenchus* Szczygieł, 1969

(Fig. 43, A–H)

#### Diagnosis

Pleurotylenchinae. Body about 0.44–0.9 mm long, slender ( $a = 27\text{--}43$  in type species). Cuticle bearing **ten longitudinal ridges** for most of its length, **lateral field ridges not differentiated**; middorsal and midventral ridges absent. Cephalic region slightly set off from body, deeply striated transversely. Stylet strong, about as long as corpus, 17–19  $\mu\text{m}$  long in type species; conus about as long as shaft; knobs prominent, 3–4  $\mu\text{m}$  across. Median bulb well developed, ovoid, with prominent refractive thickenings. Isthmus elongate-slender. Basal bulb elongate-oval, distinctly offset from intestine. **Vulva** flush with body contour, **partially covered by anterior lip flap**, at 61–64% of body length in type species. Vagina somewhat sigmoid. Postvulval uterine sac about one body width long. **Spermatheca large, axial, oval**, usually with sperm. Ovary outstretched, with oocytes in a row. Tail elongate-conoid to filiform. **Bursa indistinct or absent**. Spicules small, 16–19  $\mu\text{m}$  long in type species. Gubernaculum about one-third as long as spicule.

#### Type species

*Pleurotylenchus sachsi* (Hirschmann, 1952) Szczygieł, 1969

syn. *Tylenchus sachsi* Hirschmann, 1952

*Aglenchus sachsi* (Hirschmann) Meyl, 1961

#### Other species

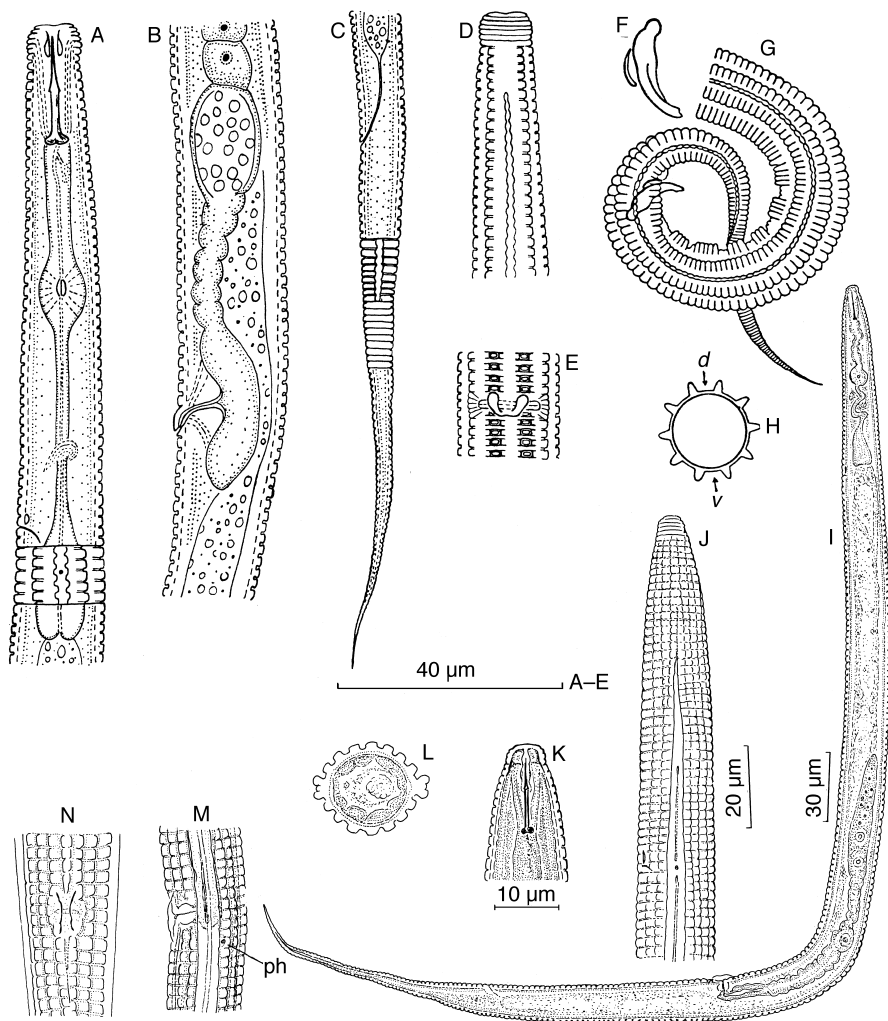
*Pleurotylenchus minor* Ebsary, 1986

#### Remarks

Andrássy (1976) proposed a subfamily for *Pleurotylenchus*. The presence of longitudinal ridges is not considered as a familial character since it is variable in members of several subfamilies, Ecphyadophoroidinae, Tylenchinae and Telotylenchinae. Geraert & Raski (1987) grouped *Cephalenchus* and *Campbellenchus* with *Eutylenchus* but, as discussed under the family Atylenchidae, the presence of cephalic setae in *Eutylenchus* removes it from the genera of Pleurotylenchinae.

ETYMOLOGY. From Greek *pleura* = side, flank, *tylos* = knob, and *enchos* = spear.

*Pleurotylenchus sachsi* was found in salt lake in Obendorf and groundwater in Erlangen suburb, West Germany (Hirschmann, 1952). Szczygieł (1969) redescribed the females collected from sandy soil around the roots of strawberry in Dabrowa Tarnowska district, Poland.



**Fig. 43.** A–H. *Pleurotylenchus sachsi* (Hirschmann). A. Oesophageal region. B. Vulval region. C. Tail. D. Head end. E. Vulva in ventral view. F. Spicule and gubernaculum. G. Tail end of male. H. Cross-section near midbody; d, dorsal; v, ventral. I–N. *Coslenchus costatus* (de Man). I–K and M. Neotype female from Breda, Holland. L and N. Female from oak soil at Luton, England. I. Entire female. J and K. Anterior ends. L. Cross-section of body. M and N. Vulval regions in lateral and ventral view, respectively. ph, prothasmid. (A–E. After Szczygiel (1969). F–H. After Hirschmann (1952). I–N. After Siddiqi (1981).)

**Genus *Cephalenchus* Goodey, 1962 (Golden, 1971)****syn. *Tylenchus* (*Cephalenchus* Goodey, 1962)*****Imphalenchus* Dhanachand & Jairajpuri, 1980**

(Figs 8(c)B; 31, E–N)

**Diagnosis**

Pleurotylenchinae. Body small to moderately large (0.4–1 mm), slender, straight to arcuate upon relaxation. Cuticle distinctly annulated, **without longitudinal ridges other than those in the lateral fields; lateral fields with six rarely four incisures at midbody**, reducing in number to four in postvulval region. Deirids just behind level of excretory pore. Prophasms dorso-sublateral, in females a little anterior to vulval level. Cephalic region small, low, rounded, offset, rarely continuous, with indistinct annules; framework with light to moderate sclerotization; labial disc indistinct, round; amphidial apertures pore-like, labial. Stylet relatively small (14–22  $\mu\text{m}$ ), but about as long as precorpus; knobs distinct. Orifice of dorsal oesophageal glands 2–3  $\mu\text{m}$  behind stylet base. Median oesophageal bulb with refractive thickenings, not offset from precorpus. Isthmus very long and slender. Basal bulb pyriform, base (mainly dorsal gland) may extend over intestine. **Vulva transverse, depressed, at 52–70% of body length, usually shifted slightly from mid-ventral line, with lateral membranes.** Postvulval uterine sac prominent. Spermatheca round to oval. Ovary outstretched, with single row of oocytes. Tails elongate-filiform, 85–236  $\mu\text{m}$  long. Male with distinct, adanal bursa often with asymmetrical flaps, a fixed rod-like gubernaculum, cephalated, pointed 15–20  $\mu\text{m}$  long spicules, and slightly raised cloacal lips.

**Type species***Cephalenchus megacephalus* Goodey, 1962syn. *Tylenchus* (*Cephalenchus*) *megacephalus* Goodey, 1962**Present status***Cephalenchus hexalineatus* (Geraert, 1962) Geraert & Goodey, 1964syn. *Tylenchus hexalineatus* Geraert, 1962*Cephalenchus hexalineatus* (Geraert, 1962) Golden, 1971*Tylenchus* (*Cephalenchus*) *megacephalus* Goodey, 1962*Cephalenchus megacephalus* (Goodey) Andr ssy, 1984*Tylenchus* (*Aglenchus*) *whitus* Egunjobi, 1967*Cephalenchus whitus* (Egunjobi) Siddiqi, 1986**Other species***Cephalenchus brevicaudatus* Raski & Geraert, 1986*C. cephalodiscus* Sultan & Jairajpuri, 1982*C. chilensis* Raski & Geraert, 1986*C. concavus* Xie & Feng, 1994*C. cylindricus* Sultan & Jairajpuri, 1982*C. daisuce* Mizukubo & Minagawa, 1985 (syn. of *C. illustris* for Ebsary, 1991)syn. *C. leptus daisuce* Mizukubo & Minagawa, 1985 (Mizukubo, 1989)*C. emarginatus* (Cobb, 1893) Geraert, 1968

- syn. *Tylenchus emarginatus* Cobb, 1893  
*Anguillulina emarginata* (Cobb) Goodey, 1932  
*C. rotundus* Siddiqui & Khan, 1983  
*C. illustris* Andrásy, 1984  
*C. imphalus* Dhanachand, Renubala & Anandi, 1993  
*C. indicus* (Dhanachand & Jairajpuri, 1980) Raski & Geraert, 1986  
 syn. *Imphalenchus indicus* Dhanachand & Jairajpuri, 1980  
*C. intermedius* Kanwar, Bajaj & Dabur, 1993  
*C. leptus* Siddiqui, 1963  
 syn. *Tylenchus* (*Cephalenchus*) *leptus* Siddiqui, 1963  
*C. leptus* (Siddiqui) Golden, 1971  
*Tylenchus* (*Filenchus*) *limichus* Nesterov, 1973  
*C. limichus* (Nesterov, 1973) Andrásy, 1984  
*C. lobus* Dhanachand & Jairajpuri, 1980  
 syn. *Cephalenchus sacchari* Maqbool, Fatima & Shahina, 1984  
*C. longicaudatus* Maqbool & Ghazala, 1986  
*C. macrodorus* (Chawla, Prasad, Khan & Nand, 1969) Raski & Geraert, 1986  
 syn. *Tylenchus* (*Aglenchus*) *macrodorus* Chawla, Prasad, Khan & Nand, 1969  
*Filenchus macrodorus* (Chawla et al.) Andrásy, 1980  
*Imphalenchus macrodorus* (Chawla et al.) Dhanachand & Jairajpuri, 1980  
*C. nemoralis* Mizukubo & Minagawa, 1985 (syn. of *C. emarginatus* for Ebsary, 1991)  
*C. planus* Siddiqui & Khan, 1983 (syn. of *C. hexalineatus* for Raski & Geraert, 1986a)  
*C. potamophilus* Mizukubo & Minagawa, 1985  
*C. tahus* Wood, 1973

## Notes

Both Golden (1971) and Siddiqui (1971) raised the subgenus *Cephalenchus*, but Golden's paper had about one month's priority in publication. *C. sacchari* is synonymized here with *C. lobus*. *Cephalenchus hexalineatus* and *C. megacephalus* have been reinstated as valid species by Andrásy (1984). Raski & Geraert (1986a) synonymized *C. limichus*, *C. planus* and *C. rotundus* with *C. leptus*, *C. hexalineatus* and *C. emarginatus*, respectively. However, *C. planus* is recognized here as a valid species. Keys to the species of *Cephalenchus* are given by Mizukubo & Minagawa (1985) and Raski & Geraert (1986a).

ETYMOLOGY. From Greek *kephalé* = head, and *enchos* = spear.

*Cephalenchus megacephalus* was collected around roots of *Musa sinensis* var. Poyo in Bardet Plantation, Adiopodoume, Côte d'Ivoire. *Cephalenchus leptus*, *C. cephalodiscus* and *C. cylindricus* were found in soils of *Pinus* spp. and fruit trees in Himalayan foothills, Uttar Pradesh, India. *Cephalenchus tahus* occurred around roots of *Festuca novaezelandiae* in the Southern Alps of New Zealand, *C. lobus* in soil of thatch grass in Imphal, in sugarcane soil in Sind, Pakistan, in fern soil in Fiji, and *C. limichus* in soil of wild plants in Moldavia. *Cephalenchus nemoralis*, *C. potamophilus*, *C. daisuce* and *C. planus* were reported from Japan.

**Genus *Campbellenchus* Wouts, 1978**

(Fig. 44)

**Diagnosis**

Pleurotylenchinae. Body moderately long (about 1 mm), straight to slightly arcuate when relaxed. **Cuticle thick, smooth, being annulated only in the short zone behind the lip region and in the male penial region enclosed within the bursa, and with 26–32 longitudinal ridges around the body** for most of its length. **Lateral field with three ridges**, which are higher than other body ridges. Amphids with small longitudinal apertures on lateral lips and large fovea. Deirids near excretory pore. Prophasms in a dorso-sublateral position, submedian, in female a little anterior to vulva. Cephalic region low, continuous, striated; labial framework not sclerotized. Stylet slender, elongate (22–34  $\mu\text{m}$  long), with small round knobs. Precorpus about as long as stylet, with straight lumen. Median bulb oval, with refractive thickenings; isthmus longer and more slender than precorpus. Basal bulb pyriform; cardia discoidal. **Vulva flush with body contour**, without lateral membranes. Spermatheca axial, twice as long as wide. **Ovary outstretched or usually with double flexures anteriorly**. Tail very long, filiform. Cloacal lips rounded, without hypopygma.

**Type species***Campbellenchus poae* Wouts, 1978**Other species***Campbellenchus filicauda* Wouts, 1978

ETYMOLOGY. From Campbell Island, and suffix of *Tylenchus*.

Both the nominal species occurred around plant roots in Campbell Island in the Southwestern Pacific Ocean, New Zealand. The type species was found in soil and on roots of *Poa litorosa* Cheesm., at Davis Point.

**Subfamily Epicharinematinae Maqbool & Shahina, 1985****Diagnosis**

Tylodoridae. Body moderately long (1–1.7 mm). Cuticle thin, annulation and lateral fields indistinct. Cephalic region elevated, dorso-ventrally flattened or rounded; labial disc absent, if present, not conspicuous. **Median oesophageal bulb well developed**, muscular, with refractive thickenings. Stylet long (23–52  $\mu\text{m}$ ) and slender, with conus being longer than the shaft, tip appearing solid. **Vagina directed forward. Postvulval uterine sac absent. Bursa flaps large, in the type genus lobed, projecting backwards**. Spicules long (39–43  $\mu\text{m}$  in type genus).

**Type genus***Epicharinema* Raski, Maggenti, Koshy & Sosamma, 1980**Other genus***Gracilancea* Siddiqi, 1976

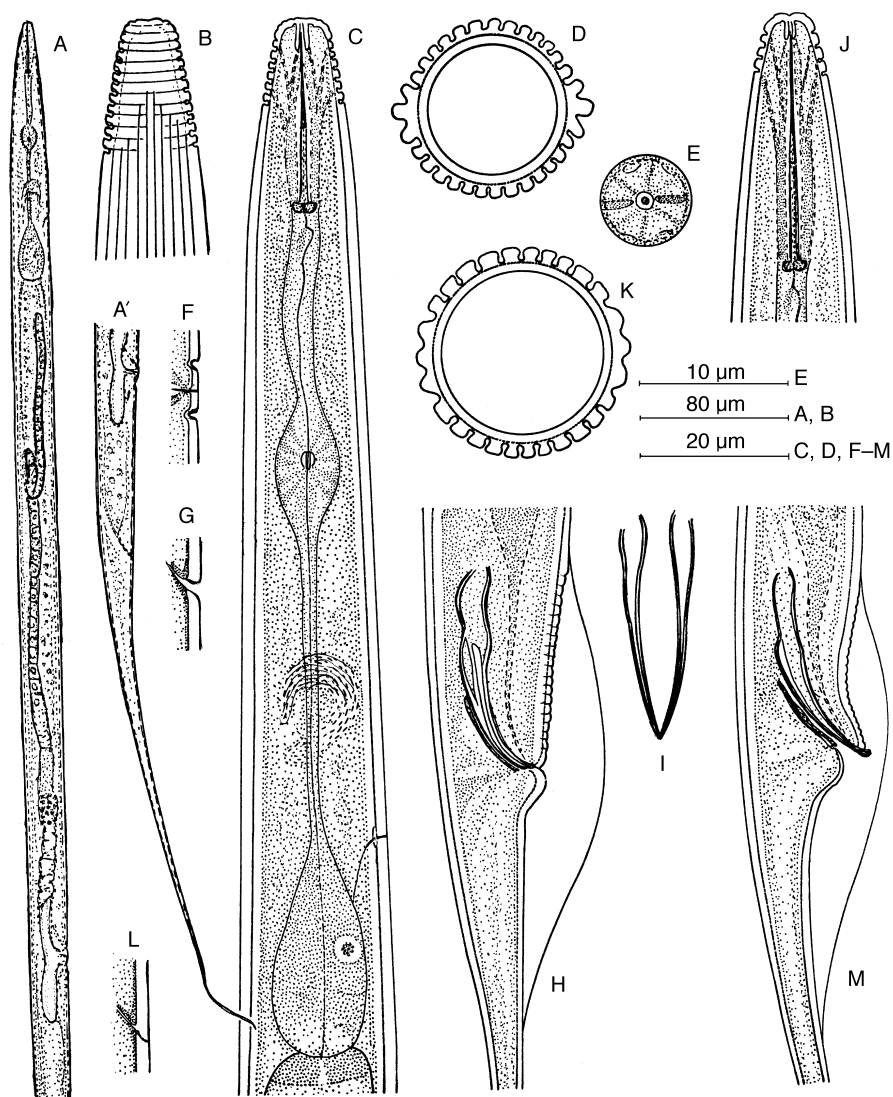


Fig. 44. A–I. *Campbellenchus poae* Wouts. J–M. *Campbellenchus filicauda* Wouts. H, I and M. Males, spicular regions, remainder females. A + A' Entire female. B and J. Head ends. C. Oesophagus. D and K. Cross-sections at midbody. E. En face view. F. Vulval region. G and L. Anal regions. (After Wouts (1978), courtesy New Zealand Journal of Zoology.)

### Key to genera of Epicharinematinae

1. Cephalic region dorso-ventrally flattened; amphids sinuate; oesophageal base partly extending over intestine ..... ***Epicharinema***  
 Cephalic region round in cross-section; amphids not sinuate; oesophageal base offset from intestine ..... ***Gracilancea***

**Genus *Epicharinema* Raski, Maggenti, Koshy & Sosamma, 1980**

(Fig. 45, A–E)

**Diagnosis**

Epicharinematinae. Cuticle smooth, lacking distinct annulation. **Cephalic region dorsoventrally flattened; front end bottle-shaped** in lateral view. **Amphidial apertures longitudinal sinuous clefts** occupying most of cephalic region. **Stylet 38–52  $\mu\text{m}$  long** in type species, with prominent round knobs. Median oesophageal bulb rounded, offset, muscular, with inner refractive thickenings; slightly posterior to middle of oesophagus. Basal bulb elongate-saccate, **dorsal gland forming a small lobe over intestine**. **Vulva marked by slight swelling, obscure**, apparently covered by cuticular flap of the anterior lip. Vagina directed forward, walls not sclerotized. **Postvulval uterine sac absent**. Spermatheca elongate-oval. Tail extremely attenuated and long. Male with body abruptly narrowed behind cloacal aperture; penial tube not formed. Bursa large, lobed; each flap with two sclerotized rib-like thickenings. Spicules almost straight. Gubernaculum 8–14  $\mu\text{m}$  long, slender.

**Type species**

*Epicharinema keralense* Raski, Maggenti, Koshy & Sosamma, 1980

No other species.

ETYMOLOGY. Greek *epicharis* = pretty, beautiful, and *nema* = nematode.

The type species was found around roots of coconut palm, *Cocos nucifera* L., at Kayangulam, Kerala State, India.

**Genus *Gracilancea* Siddiqi, 1976**

(Fig. 45, F–J)

**Diagnosis**

Epicharinematinae. Body about 1 mm long. Cuticle thin, marked with indistinct striae. Cephalic region continuous, rounded; a small labial disc present; framework lightly sclerotized, its **inner margins forming a large bulboid stylet-guiding tube**. Amphids small with circular pores near oral disc. **Stylet slender, 23–28  $\mu\text{m}$  long in type species; conus needle-like, slightly longer than the shaft**; basal knobs rounded. Median oesophageal bulb muscular, with refractive thickenings. Basal bulb saccate with flat base; cardia large, rounded. **Vulva transverse, flush with body contour, with lateral membranes**. **Vagina directed forward, sclerotized**. **Postvulval uterine sac absent**. Spermatheca oval. Tail very long, regularly tapering to a filiform tip. Spicules 22–24  $\mu\text{m}$  long. Bursa simple, adanal.

**Type species**

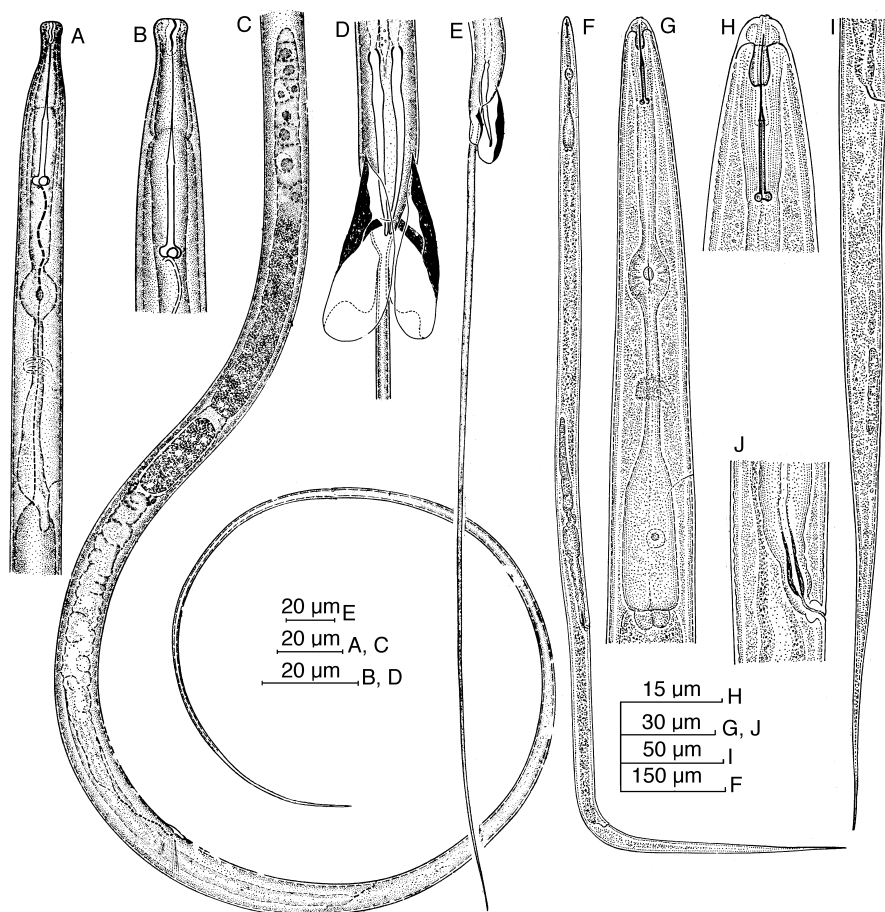
*Gracilancea graciloides* (Micoletzky, 1925) Siddiqi, 1976

syn. *Tylenchus graciloides* Micoletzky, 1925

*Anguillulina graciloides* (Micoletzky) Goodey, 1932

*Filenchus graciloides* (Micoletzky) Meyl, 1961

No other species.



**Fig. 45.** A–E. *Epicharinema keralense* Raski, Maggenti, Koshy & Sosamma. F–J. *Gracilancea graciloides* (Micoletzky), lectotype female. A and G. Oesophageal regions of females. B and H. Head ends of females. C. Posterior region of female. D. Bursa region in ventral view. E. Male tail. F. Female. I. Female tail. J. Vulval region. (A–E. After Raski *et al.* (1980), courtesy *Revue de Nématologie*. F–J. After Siddiqi (1976), courtesy *Nematologica*.)

#### Note

Siddiqi (1976) designated a lectotype for *G. graciloides* and gave a description of it.

ETYMOLOGY. From Latin, *gracilis* = thin, and lance (for thin stylet).

The type species was found in sod with *Carex* grass in a meadow near Lake Tjustруп, Denmark. It also occurs in Russia and Poland.



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# V

## Infraorder Anguinata

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### INFRAORDER ANGUINATA INFRAORD. N.

#### Diagnosis

Tylenchina. Small to large sized (0.4–3.5 mm), in some genera adults may be obese and sedentary. **No marked sexual dimorphism in anterior region. Cuticle with fine transverse striations, often appearing smooth.** Lateral field plain, or with four, six or more incisures. Deirids usually present. **Phasmids absent; prophasms present in postmedian region outside lateral field, in female near vulva. Cephalic region low, cap-like, smooth** with indistinct or no annulations, generally continuous with body contour; **framework hexaradiate, with or without faint sclerotization.** Oral opening a small round pore surrounded by six labial papillae; amphids indistinct, oval, slit-like, slightly dorso-sublateral on raised areas on labial plate but at some distance from oral opening. **Stylet small (under 15  $\mu\text{m}$ ), with small rounded knobs.** Orifice of dorsal gland close to stylet base. Median oesophageal bulb present or absent, with or without refractive thickenings. Oesophageal glands tend to be enlarged, forming a basal bulb, or rarely, the dorsal gland extends over intestine dorsally and laterally; **no stem-like extension at base of basal bulb. Cardia absent; two anteriormost intestinal cells often acting as a valve.** Gonads single, anteriorly outstretched, may be reflexed or coiled in swollen adults; rarely germ cells may be arranged about a rachis. Vulva a large transverse slit, posteriorly located; lateral vulval membranes distinct only in *Pterotylenchus*. **Spermatheca axial, elongated, sac-like** (except rounded in *Pseudhalenchus*). Sphincter valve between oviduct and uterus may be present. A postvulval sac often longer than body width present (absent in *Diptenchus*), may serve as storage for sperm. **Sperm round, large, with a prominent translucent cytoplasmic vesicle around the nucleus. Spicules robust, anteriorly expanded,** separate or fused medially, tip often truncate or broadly rounded. Gubernaculum simple, trough-like, not protrusible, rarely absent (as in *Nothanguina*). Bursa moderately large, usually subterminal, but may extend to terminus (Sychnotylenchidae) or be adanal. Tails similar between

sexes (except when bursa is terminal), usually elongate-conoid, may be cylindroid or filiform; juvenile tails often elongate-conoid to filiform. **Fungal feeders or parasites of lower (mosses, seaweeds) and higher plants, attacking stems, leaves, floral parts and seeds, almost always inciting galls;** root parasitism known only for *Subanguina radiculicola*, which incites and inhabits galls; also associates of insects (Sychnotylenchidae) but not parasitic in insects or other animals.

#### Type genus

*Anguina* Scopoli, 1777

#### Type superfamily

Anguinoidea Nicoll, 1935 (1926)

No other superfamily.

#### Relationship

Anguinata differ from Tylenchata in having their origin from fungal-feeding forms and hence they represent a different line of evolution as indicated by their morphological and ecological development. They are not root parasites (except *Subanguina radiculicola* which lives in root galls) but are either fungal feeders or parasites of above-ground plant parts such as stems, leaves, buds and seeds. Their closest relatives are Hexatylini which have become parasites of insects and mites, but some still have a free-living, mycetophagous generation.

### **SUPERFAMILY ANGUINOIDEA NICOLL, 1935 (1926)**

**syn. Anguillulinoidea Baylis & Daubney, 1926 (Nicoll, 1935)**

**Nothotylenchoidea Thorne, 1941 (Jairajpuri & Siddiqi, 1969)**

#### Diagnosis

With characters of the infraorder Anguinata.

#### Type genus

*Anguina* Scopoli, 1777

#### Type family

Anguinidae Nicoll, 1935 (1926)

#### Other family

Sychnotylenchidae Paramonov, 1967

#### Relationship

Traditionally *Anguina* and *Ditylenchus* have been classified in the Tylenchidae, but they differ from the members of this family in their different origin and evolution from fungal-feeding forms and in having two anteriormost cells of the intestine modified to act as a valve (a tricellular cardia is absent in this group), a prominent cristaformeria and large-sized sperm with a prominent cytoplasmic vesicle. Members of the Anguinoidea are closely similar to those of the Paurodontidae and

free-living forms of the Sphaerularioidea (suborder Hexatyline). Siddiqi (1984) pointed out that Anguinoidea was a relative of Sphaerularioidea and he (1986) assigned it to the suborder Hexatyline.

Sturhan & Rahi (1996) found the prothasms in Anguinoidea and this finding brings them close to Tylenchoidea. They considered Anguinidae as a family of Tylenchoidea which includes all the genera with these phasmid-like structures dorsal of the lateral fields and well anterior to the tail. However, due to their separate origin and evolutionary trends, anguinids are considered here as a separate infra-order Anguinata.

### Key to families of Anguinoidea

1. Female tail cylindroid or subcylindroid, dissimilar to that of male; bursa enveloping tail terminus; associates of insects ..... **Sychnotylenchidae**
- Female tail conoid to filiform, rarely subcylindroid, similar to that of male; bursa not enveloping tail terminus; very rarely associates of insects .. **Anguinidae**

## FAMILY ANGUINIDAE

### (Fungal feeders and parasites of aerial parts of plants)

The family differs from the Hexatyline in lacking an entomoparasitic phase in the life history and from the Tylenchina in being fungal feeders and parasites of the aerial parts of plants. Like Hexatyline, the ancestral trait of the Anguinidae is fungal-feeding. A number of genera (*Anguina*, *Subanguina*, *Nothanguina*, *Ditylenchus*, *Pterotylenchus*) contain species which are economically important plant parasites.

*Anguina tritici* (wheat-gall nematode) was the first plant-parasitic nematode to be recorded; juveniles of this species were discovered by Needham (1744) in a wheat seed-gall. The ear-cockle disease of wheat caused by *Anguina tritici* has been eliminated from most of the developed countries but it still takes its toll in less developed countries (China, India, Iran, etc.), where crop losses may sometimes be as much as 30%. The control lies in the elimination of cockles or galled grains from seeds at the time of sowing.

In *A. tritici*, *A. agrostis* and *A. graminis* the second-stage juvenile is the resistant and infective stage, which can withstand desiccation for years.

*Subanguina millefolii* and *Subanguina mobilis* are said to have the third-stage juvenile as infective. The fourth-stage juvenile is the most resistant in the case of forms such as *Ditylenchus phyllobia* and *Ditylenchus dipsaci* and several species of *Subanguina*. Finally, in *Subanguina radiculicola* and *S. danthoniae* the adults remain dormant in the dried galls on the grass. Upon soaking, the nematodes revive, and attack the plant, reaching the aerial parts as the plant grows, by moving through water films on the exterior, or migrating through the plant tissues.

*Anguina tritici* may feed ectoparasitically on the growing points and leaf bases until it is able to enter the inflorescence. As the embryo seeds are formed, the nematodes invade them and adults feed and mate inside the grain. The female lays a large number of eggs (a few hundred to 32,000). The adults die in the galled grain, whose entire cavity is then occupied by the second-stage juveniles.

*Anguina agrostis* causes galls on flowers and seeds of several grasses (*Agrostis*, *Festuca*, *Lolium*, *Poa*, etc.) in Europe, North America, Australia and New Zealand. Parasitized inflorescences and flowers of *Agrostis* are so altered in shape that a new species *Agrostis sylvatica* Huds. was described (Southey, 1973). *Anguina funesta* (?syn. of *A. agrostis*) produces seed-galls on rye grass (*Lolium rigidum*) in Australia and is a vector of a toxin-producing bacterium, *Clavibacter toxicus* (*Corynebacterium rathayi*).

The infective-stage juveniles of *Anguina funesta* carry *Clavibacter toxicus* attached to their cuticle to rye grass ears (Bird, 1985). The nematode attacks the seeds and lies dormant inside them. The bacterium produces toxins that kill sheep grazing in infested grass in Australia. The cuticle and excretory pore secretions of second-stage dauer juveniles of *A. funesta* produce macromolecules that bind wheat germ agglutinin, indicating that accessible *N*-acetyl-D-glucosamine residues are present on these structures, and form a covering over the cuticle surface on the body. This protective secretion from the excretory system is more actively produced when the cuticle surface is covered by bacteria (Bird *et al.*, 1989). Since the nematode is carried within the seed, rye grass seeds from infested regions, particularly in Australia and New Zealand, are subjected to strict quarantine regulations. The bacteria-infested galls are yellow in colour, the toxin being located primarily in the wall of the gall. About 1000 galls, if eaten by sheep, are deadly; the livestock poisoning is known as flood plain staggers. The meat industry of Australia is concerned, as many sheep die due to grazing on infested grass, and has sanctioned large sums of money for research into this problem. A similar nematode-bacterium interaction is found in the 'Tundu' disease of wheat caused by *A. tritici* and *Corynebacterium tritici* together, but without any poisonous effects.

*Subanguina radicicola* is the only known anguinoid that parasitizes roots. It induces galls on roots of several grasses, barley and rye and occurs widely in Europe. Galls range from 0.5 to 6 mm long and contain a single generation of nematodes. *Subanguina plantaginis* parasitizes bracted plantain, *Plantago aristata* Mich., in USA. It causes galling of leaves and flowers, and looping of peduncles; extreme infections causing death of the plant.

Quiescent third-stage juveniles of *Subanguina chrysopogoni* can survive for more than 9 months in a desiccator, refrigerator or at room temperature in air-dried galls. They moult to the fourth stage before penetrating the growing points of *Chrysopogon fulvus* seedlings (Bajaj *et al.*, 1990). *Subanguina danthoniae* causes leaf-galls on *Danthonia californica*, which are round, green to straw-yellow in colour and are found singly or in groups of 50 or more. The maximum number of adults found in one gall was 19. Since only the adults are found in mature galls, Maggenti *et al.* (1974) believed that the adults are the resistant stage, capable of surviving within the gall for 1 or 2 years. The cryptobiosis of the adults in mature galls is an unusual feature of the subfamily. The second-stage infective juveniles migrate to the soil to re-infect the grass tissue.

*Ditylenchus dipsaci*, popularly called stem nematode or stem and bulb nematode, attacks over 450 plant species, mostly in cooler parts of the world. It occurs in biological races or biotypes (about a dozen are known, some have been described as new species), and is pathogenic to a variety of field crops, such as beans, lucerne, maize, narcissus, oats, onion, rye, strawberry and tulip. It was originally described from teasel, *Dipsacus fullonum* L., from Germany. The nematodes revived after 23

years when dried teasel heads were soaked in water by Fielding (1951). The fourth-stage juvenile is the surviving stage. In drying plant tissues the nematodes tend to aggregate and when dried form 'eelworm wool'.

The nematode is a migratory endoparasite of bulbs and green parts of plants and causes dissolution of the middle lamella of the cell walls so that cells become detached and tissue swells. The life cycle on onion is completed in 19–23 days at 15°C, the female laying 207–498 eggs and surviving for 45–73 days (Yüksel, 1960). At least four karyotypes with  $2n = 12, 24, 54$  and 60 chromosomes are known; a giant race attacking *Vicia faba* has  $2n = 36–56$ .

*Ditylenchus dipsaci* transmits *Corynebacterium insidiosum* (McCull.) Jensen, the causal agent of a bacterial wilt in lucerne (alfalfa), and is known to predispose wilt resistance in this crop. Fumigation of infested soil and seedbeds and hot water treatment of bulbs at 44–45°C for 3 h gives a reasonable control.

*Ditylenchus angustus* is another important pest nematode. It attacks rice in Southeast Asia and some parts of Africa, and causes 'ufra' disease. On growing rice, the nematodes feed ectoparasitically on the newly formed tissues, and on mature plants they are found in the tender parts of the stem, leaf sheath, stalks, sterile twisted grains and in the malformed peduncle. The largest populations occur during June to November in Bangladesh and throughout the winter months, during which more than three generations are produced. The life cycle from egg to egg took 8 days and the duration of second-, third- and fourth-stage juveniles was 1, 1 and 2 days, respectively (Ali & Ishibashi, 1997). The nematodes lie dormant within the dry glumes and stubble and can survive desiccation for more than a year. Approximately 8000 tonnes of rice were estimated to have been lost due to this nematode in the Noakhali region of Bengal in 1910 (Butler, 1913), and 50% and 20–90% crop losses due to 'ufra' are estimated for Bangladesh and Thailand, respectively (see Seshadri & Dasgupta, 1975). In lowland rice, *D. angustus* causes 60–70%, 20–90% and 50–100% losses in Bangladesh, Thailand and Vietnam, respectively. Adults and third- and fourth-stage juveniles are the survival stages and since the fourth stage predominates in infested plant material it is probably the principal survival and infective stage (Ibrahim & Perry, 1993). *Ditylenchus drepanocercus* was found associated with the leaf-blotch of *Evodia roxburghiana*, an Indian evergreen tree.

These species of *Ditylenchus* and several others constitute the *D. dipsaci* group which have four incisures in the lateral field, have sharply pointed tail tips, are plant-cell feeders and have almost abandoned their primitive trait of fungal feeding. The other group, the *D. trififormis* group, which includes most *Ditylenchus* species, is basically fungal feeding and has six incisures in the lateral field and a round end tail tip. The group is a close relative of *Safranema* which has the characteristics of this group, but has the dorsal gland forming a long lobe over the intestine. Some species of this group and of *Safranema* occur in insect galleries where they probably feed on fungi.

A few species of the *D. trififormis* group are also economically important. *Ditylenchus destructor*, the potato tuber nematode, or potato-rot nematode, is noted as an important pest of potato and bulbous iris in Europe and North America. It is a voracious fungal feeder and can be cultured easily. *Ditylenchus myceliophagus* is important because it destroys the mycelium of the cultivated mushroom, *Agaricus bisporus*. Peak populations of nematodes are found shortly before the last mycelium is killed.

The nematodes migrate, but if there is not enough moisture, they congregate in masses on the mushroom culture boxes, on the casing, or they may hang down like miniature stalactites. The nematode is controlled by the pre-treatment of compost, which involves 'peak-heating' before the spawning and 'cooking-out' of spent beds after lifting the crop. However, nematodes of this group are not parasites of aerial parts of plants as compared to the *D. dipsaci* group.

*Orrina phyllobia* (= *Nothanguina phyllobia*) produces leaf-galls on silverleaf nightshade (*Solanum elaeagnifolium*), an economically troublesome perennial weed in cotton production, in south-west USA. It is also found on this host in India. Siddiqi & Lenné (1984) described a stem-gall nematode, *Pterotylenchus cecidogenus*, which is an important parasite of a tropical pasture legume, *Desmodium ovalifolium* Wall., in Colombia.

Paramonov (1967) proposed the genus *Subanguina* with *Subanguina radiculicola* as type species and he (1970) stated that *S. radiculicola* retained the ancestral type of ontogeny, suggesting that the forerunners of *Ditylenchus* and *Anguina* were not yet differentiated and remained in the rhizosphere. Later, the early *Anguina* forms moved into the green organs of plants and subsequently attacked and occupied the gametophytes. This departure from the root into the aerial parts of plants freed the Anguininae of their links with the saprobiotic environment, thereby reducing juvenile mortality, and increasing their chances of survival.

Paramonov (1970) held the view that the Anguininae comprised only *Anguina*, *Subanguina* and *Nothanguina* and that *Ditylenchus* belonged in the Tylenchinae. He believed that Tylenchoidea showed two evolutionary lines, one relinquishing mycetophagy for root parasitism (i.e. the *Tylenchus* line) and the other retaining mycetophagy but advancing also to parasitism of the aerial parts (i.e. the *Ditylenchus* line). Paramonov noticed the obvious similarity in the general organization of *Ditylenchus* and *Anguina* and stated, 'We will not be far wrong if we assume that *Anguina* and *Ditylenchus* are phyletically close and that *Anguina* a very specialized branch which arose from ditylenchoid forerunners'. Even so, Paramonov did not fully realize the separate origins and evolutions of Tylenchoidea and Anguinoidea.

*Anguina* Scopoli, 1777, is the seniormost genus in Tylenchida. Chitwood (1935) discussed the status and seniority of *Anguina* and reduced *Anguillulina* Gervais & Van Beneden, 1859 to a junior objective synonym of it. The two genera had the same type species and, although *Anguillulina* had gained wide acceptance, the International Commission on Zoological Nomenclature accepted the name *Anguina* as valid and *Anguillulina* as an invalid rejected name in Zoology (1958, opinions 329 and 341). Nicoll (1935) proposed Anguinidae as a new family name for *Anguina* because it had priority over *Anguillulina* and *Tylenchus*, and thus he proposed it to replace family names Anguillulinidae and Tylenchidae. Similarly, Anguinoidea was mentioned by Nicoll as a name to replace Anguillulinoidea. *Paranguina* Kirjanova, 1955 and *Heteroanguina* Chizhov, 1980 were synonymized by Brzeski (1981) with *Anguina* and *Subanguina*, respectively. *Heteroanguina* was proposed by Chizhov (1980) with *Heteroanguina graminophila* as a new combination and the only species in the genus.

Siddiqi (1971) defined Anguinidae and differentiated it from Tylenchidae. Thus, *Ditylenchus* and *Tylenchus*, which were placed together under Tylenchidae/Tylenchinae for a long time, were separated into two different families. Golden's

(1971) proposal of *Ditylenchinae* was not accepted by Siddiqi (1980a) since the genus *Ditylenchus* is so similar to *Anguina*. *Ditylenchinae* was raised to family by Fotedar & Handoo (1978) and by Skarbilovich (1980).

*Safianema* was proposed as a junior synonym of *Pseudhalenchus*, and *Pseudhalenchinae* transferred to *Belonolaimidae* by Ryss & Krall (1981). The genera *Safianema* and *Diptenchus* were synonymized with *Ditylenchus* by Fortuner (1982). These actions are not accepted here. As mentioned above, *Safianema* is close to the *Ditylenchus triformis* group in having six incisures in the lateral field and a rounded tail tip and in being a fungal feeder, the characters which differentiate it from the *Ditylenchus dipsaci* group. Further work is needed to decide the systematic positions of the species of these groups. At present, *Safianema* is recognized by the character of the oesophageal glands forming a lobe overlapping the intestine, two anterior cells of intestine forming a rounded cardia and the anteriormost part of intestine narrow and lacking a lumen, and *Diptenchus* is considered a valid genus because it lacks a postvulval uterine sac which is a characteristic for all the Anguinidae.

In their revision of Anguininae, Chizhov & Subbotin (1985) stressed the trophic specialization of its members. According to them *Anguina*, *Paranguina* and *Subanguina* are parasites of monocotyledonous plants having a broad range of hosts. They cause hypertrophy and hyperplasia of the host tissue resulting in coloured, ovoid galls, produce one generation per gall and have the second-stage juvenile as the invasive stage. Species of *Mesoanguina* Chizhov & Subbotin, 1985, on the other hand, have a narrow host specificity, cause hypertrophy and hyperplasia of affected tissue producing colourless, often hairy galls, have two morphologically distinct generations per gall and their third-stage juvenile is the invasive stage. *Heteroanguina* spp. are parasites of both monocots and dicots causing various coloured and shaped galls, produce one generation per gall and their fourth-stage juvenile is the invasive stage.

The differentiation between *Anguina*, *Subanguina*, *Heteroanguina* and *Mesoanguina* is becoming increasingly difficult (see Choi & Loof, 1974; Fortuner & Maggenti, 1987). Fortuner & Maggenti (1987) reviewed the family Anguinidae and synonymized *Nothanguina* with *Anguina* and *Heteroanguina*, *Afrina* and *Mesoanguina* with *Subanguina*. They did not give due taxonomic importance to the differences in host preferences, gall staining, infective juvenile stages and number of generations in a gall and the characters of the presence/absence of a muscular median oesophageal bulb (*Anguina*/*Nothanguina*, *Ditylenchus*/*Nothotylenchus*) and the overlapping oesophageal glands (*Ditylenchus*/*Safianema*/*Orrina*).

Brzeski (1981) had proposed the synonymy of *Heteroanguina* and *Subanguina*. Chizhov & Subbotin (1985) re-defined *Heteroanguina* and proposed the genus *Mesoanguina*, with *M. millefolii* as the type species. Fortuner & Maggenti (1987) synonymized *Mesoanguina* with *Subanguina*. I agree with this action because *Mesoanguina* is based mainly on the biological and host preference characters and there are no stable morphological characters to support them. Ebsary (1991) accepted the synonymy of *Heteroanguina*, *Afrina* and *Mesoanguina* with *Subanguina*. *Afrina* was synonymized with *Anguina* by Siddiqi (1986) and Chizhov & Subbotin (1990) accepted this action. Fortuner & Maggenti (1987) re-examined paratypes of *A. hyperrheniae* and found that oocytes were arranged in one to two rows and not in multiple rows as in *Anguina*. Although the species shows many similarities with *Anguina*, it is

considered here as a species of *Subanguina* on the character of the genital system and consequently *Afrina* is considered a junior synonym of *Subanguina*.

*Cynipanguina* was regarded as a synonym of *Anguina* by Brzeski (1981) and Chizhov & Subbotin (1985, 1990). The type and only species of *Cynipanguina*, *C. danthoniae*, morphologically is very similar to those of *Subanguina* except that it has a digit-like extension of the oesophageal base and the isthmus is offset from the basal bulb by a constriction. The importance of digit-like extension of the oesophageal base was stressed by Maggenti *et al.* (1974) when they proposed *Cynipanguina*, but Brzeski (1981) considered it to be an artefact. Fortuner & Maggenti (1987) stressed the importance of the oesophageal character and reinstated *Cynipanguina*. In endoparasitic, swollen females of *Subanguina* and *Anguina*, which have well-developed median and oesophageal bulbs, the characters of the shape of the isthmus and bulb cannot be used at generic level. Siddiqi (1986) illustrated a digit-like extension of the basal bulb for *Subanguina radiculicola* and an isthmus offset from the median bulb by a constriction in *A. tritici*. The genital system of the female and the character of the adults being cryptobiotic are similar to *Subanguina radiculicola*. *Cynipanguina danthoniae* thus belongs in the genus *Subanguina* and *Cynipanguina* is therefore synonymized with it.

## Family Anguinidae Nicoll, 1935 (1926)

syn. Anguillulinidae Baylis & Daubney, 1926

Anguinidae Paramonov, 1962 (Siddiqi, 1971)

Ditylenchidae Golden, 1971 (Fotedar & Handoo, 1978)

Nothotylenchidae Thorne, 1941 (Jairajpuri & Siddiqi, 1969)

### Diagnosis

Anguinoidea. Adults from about 0.4 to 3 mm long, slender or obese. Cephalic region low, smooth; framework hexaradiate, sectors almost equal. Muscular valvate median bulb present or absent. Basal oesophageal bulb small or large, offset from intestine, or the dorsal gland may become enlarged and extend over intestine as a lobe. Excretory duct not abnormally widened or sclerotized. Vulva generally at less than 85% of body length. Postvulval uterine sac present, or rarely (e.g. *Diptenchus*) absent. Ovary outstretched or reflexed; oocytes may be arranged about a rachis in obese females. **Tails similar between sexes, female tail rarely subcylindrical, never cylindrical or hooked.** Bursa variable from adanal to subterminal, **never enclosing tail tip.** Fungus feeders or parasites of stem, leaves, flower parts and seeds, where they usually incite galls, not root parasites (except *Subanguina radiculicola* which incites and inhabits root-galls).

### Type subfamily

Anguininae Nicoll, 1935 (1926)

### Other subfamily

Halenchinae Jairajpuri & Siddiqi, 1969

### Remarks

Fortuner (1984) discussed the position of Anguinidae in relation to Anguillulinidae. Baylis & Daubney (1926) proposed the Anguillulinidae for *Anguillulina* Gervais &



Van Beneden, 1859, with which they synonymized *Tylenchus* Bastian, 1865. Chitwood (1935) re-established *Anguina* Scopoli, 1777, designated *A. tritici* (Steinbuch, 1799) as its type species, and considered *Anguillulina* as a junior objective synonym of *Anguina*.

Anguilluliniidae is not acceptable under the provision of the Article 40(b) of the ICZN. The date of the rejected name, however, is to be included within the parentheses after the year of the establishment of the Anguinidae as per ICZN Recommendation 40(A). Paramonov (1962) also proposed Anguininae which was raised to family by Siddiqi (1971). Pseudhalenchinae Siddiqi, 1971 is synonymized here with Anguininae since *Pseudhalenchus* is closely related to *Safianema* and *Ditylenchus*.

### Key to subfamilies of Anguinidae

1. Excretory duct widened, sclerotized; exclusively marine, parasitic on sea algae forming galls ..... **Halenchinae**
- Excretory duct not widened or sclerotized; not marine; not parasitic on sea algae ..... **Anguininae**

### Subfamily Anguininae Nicoll, 1935 (1926)

**syn. Anguillulinae Baylis & Daubney, 1926**

**Anguininae Paramonov, 1962**

**Cynipanguininae Fotedar & Handoo, 1978**

**Ditylenchinae Golden, 1971**

**Nothanguininae Fotedar & Handoo, 1978**

**Nothotylenchinae Thorne, 1941**

**Pseudhalenchinae Siddiqi, 1971**

### Diagnosis

Anguinidae. Adults slender or obese, straight, arcuate or strongly curved when relaxed. Precorpus cylindroid. Postcorpus muscular or non-muscular. **Basal bulb enclosing oesophageal glands present**, dorsal gland may form a lobe extending over intestine dorsally and/or sublaterally (*Pseudhalenchus*, *Safianema*, some *Anguina*). Vulva lacking lateral membranes (except *Pterotylenchus*). Postvulval uterine sac well developed (absent in *Diptenchus*). Crustaformeria with four or more rows of cells. Ovary outstretched or with tip reflexed once or twice; oocytes in rows or arranged about a rachis. Gubernaculum present.

### Type genus

*Anguina* Scopoli, 1777

### Other genera

*Diptenchus* Khan, Chawla & Seshadri, 1969

*Ditylenchus* Filipjev, 1936

*Indoditylenchus* Sinha, Choudhury & Baqri, 1985

*Nothanguina* Whitehead, 1959

*Nothotylenchus* Thorne, 1941

*Orrina* Brzeski, 1981

*Pseudhalenchus* Tarjan, 1958  
*Pterotylenchus* Siddiqi & Lenné, 1984  
*Safianema* Siddiqi, 1980  
*Subanguina* Paramonov, 1967

### Key to genera of Anguininae

1. Female obese; crustaformeria with more than 20 cells ..... 2  
     Female not obese; crustaformeria with less than 20 cells (generally with 16 cells) ..... 4
2. Female strongly obese and spirally curved; gametocytes usually arranged about a rachis; columella cells in more than four rows ..... 3  
     Female not strongly obese or spirally curved; gametocytes not arranged about a rachis; columella cells in four rows ..... *Subanguina*
3. Median oesophageal bulb strongly developed, muscular ..... *Anguina*  
     Median oesophageal bulb absent ..... *Nothanguina*
4. Dorsal oesophageal gland forming a long lobe extending over intestine, with nucleus lying posterior to oesophago-intestinal junction; anteriormost two intestinal cells forming a cardia-like rounded structure; lumen of anterior region of intestine absent ..... 5  
     Dorsal oesophageal gland not forming a long lobe extending over intestine, with nucleus lying anterior to oesophago-intestinal junction; anteriormost two intestinal cells not forming a cardia-like rounded structure; lumen of anterior region of intestine present ..... 8
5. Lateral vulval flaps present ..... *Pterotylenchus*  
     Lateral vulval flaps absent ..... 6
6. Spermatheca rounded; sperm small-sized ..... *Pseudhalenchus*  
     Spermatheca elongate; sperm large-sized ..... 7
7. Lateral field with four incisures, plant gall-inciting ..... *Orrina*  
     Lateral field with six incisures; fungal feeders ..... *Safianema*
8. Postvulval uterine sac absent ..... *Diptenchenus*  
     Postvulval uterine sac present ..... 9
9. Excretory pore anterior to median oesophageal bulb ..... *Indoditylenchus*  
     Excretory pore posterior to median oesophageal bulb ..... 10
10. Median oesophageal bulb distinct, muscular ..... *Ditylenchus*  
     Median oesophageal bulb indistinct, non-muscular ..... *Nothoditylenchus*

**Genus *Anguina* Scopoli, 1777**

syn. *Angvina* (= original spelling amended to *Anguina* by later workers)

*Anguillulina* Gervais & Van Beneden, 1859 (= objective synonym)

*Anguillulina* (*Anguina* Scopoli) (Schneider, 1939)

*Paranguina* Kirjanova, 1954 (= nomen nudum)

*Paranguina* Kirjanova, 1955

(Fig. 46)

**Diagnosis**

Anguininae. Medium- to large-sized (1–2.7 mm), obese; **mature female curved generally in one to one-and-a-half spirals. Median oesophageal bulb muscular.** Basal bulb in adults enlarged, continuous or offset from isthmus by a constriction, base usually extending over anterior end of intestine. Ovary with one or two flexures anteriorly due to excessive growth; **oocytes in multiple rows, arranged about a rachis. Crustaformeria a long tube formed by a large number of cells in multiple irregular rows.** Spermatogonia in multiple rows. Bursa subterminal. Second-stage juvenile generally resistant and is the infective stage. Obligate plant parasites inciting galls in seeds of cereals and grasses, stems, leaves and inflorescence of various monocotyledonous plants; type species causes wheat seed-galls (ear cockles); only *A. amsinckiae* and *A. balsamophila* parasitize dicotyledonous plants.

**Type species**

(Subsequent designation by Chitwood, 1935)

*Anguina tritici* (Steinbuch, 1799) Filipjev, 1936

syn. *Vibrio tritici* Steinbuch, 1799

*Rhabditis tritici* (Steinbuch) Dujardin, 1845

*Anguillula tritici* (Steinbuch) Grube, 1849

*Anguillulina tritici* (Steinbuch) Gervais & Van Beneden, 1859

*Tylenchus tritici* (Steinbuch) Bastian, 1865

*Anguillula scandens* Schneider, 1866

*Tylenchus scandens* (Schneider) Cobb, 1890

*Anguillulina scandens* (Schneider) Goodey, 1932

**Other species**

*Anguina agropyri* Kirjanova, 1955

syn. *Paranguina agropyri* Kirjanova, 1955

*Anguina pacificae* Cid del Prado Vera & Maggenti, 1984 (syn. by Chizhov & Subbotin, 1990)

*A. agropyronifloris* Norton, 1965 (syn. of *A. agrostis* for Chizhov & Subbotin, 1990)

*A. agrostis* (Steinbuch, 1799) Filipjev, 1936

syn. *Vibrio agrostis* Steinbuch, 1799

*Anguillula agrostis* (Steinbuch) Ehrenberg, 1838

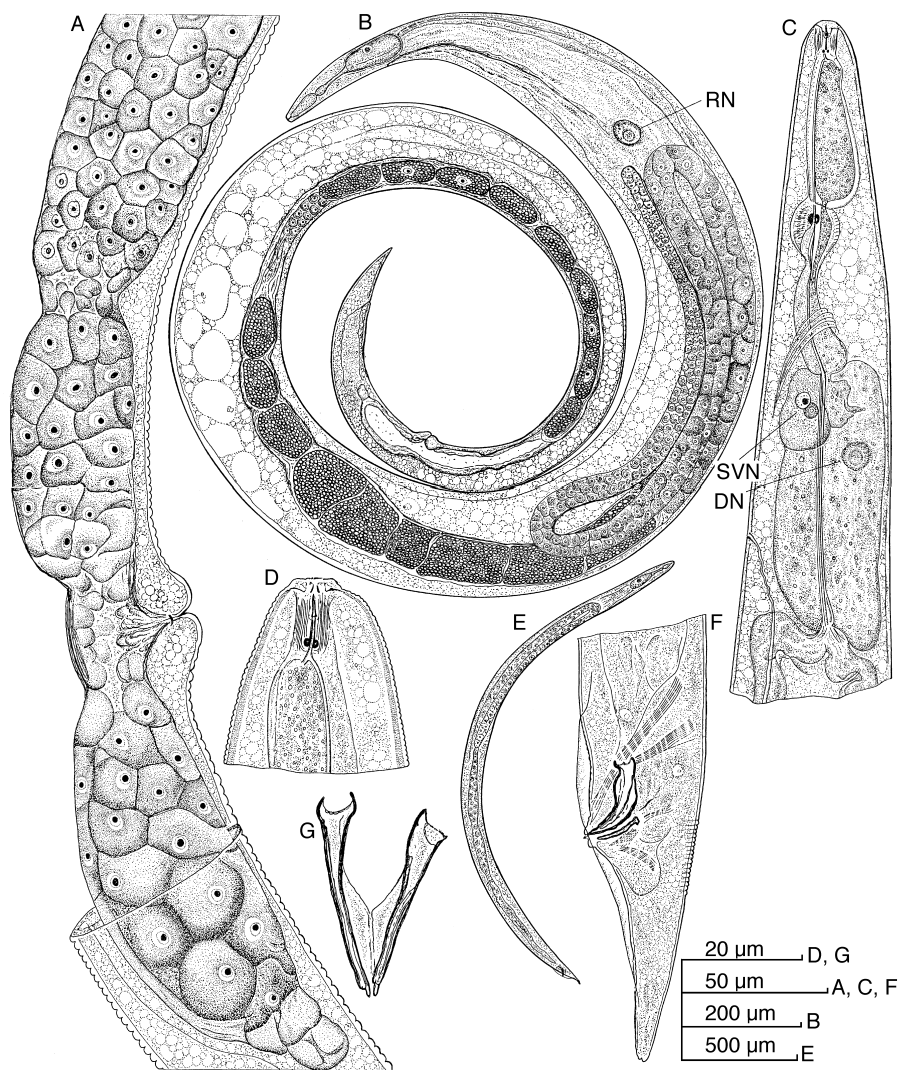
*Tylenchus agrostis* (Steinbuch) Goodey, 1930

*Anguillulina agrostis* (Steinbuch) Goodey, 1932

*Vibrio phalaridis* Steinbuch, 1799

*Anguillula phalaridis* (Steinbuch) Ehrenberg, 1838

*Tylenchus phalaridis* (Steinbuch) Örley, 1880



**Fig. 46.** *Anguina tritici* (Steinbuch) from wheat grain. A. Vulval region showing surface view of uterus and postvulval uterine sac. B. Female. C. Oesophageal region of male. D. Head end of female. E. Male. F. Tail end of male. G. Spicules. (DN, nucleus of dorsal oesophageal gland; SVN, nuclei of subventral glands; RN, nucleus of renette cell.)

(syn.) *Anguillulina phalaridis* (Steinbuch) Goodey, 1932  
*Anguina phalaridis* (Steinbuch) Chizhov, 1980  
*Tylenchus agrostidis* Bastian, 1865  
*Anguillula agrostidis* (Bastian) Warming, 1877  
*Tylenchus phlei* Horn, 1888  
*Anguina poophila* Kirjanova, 1952  
*Anguina lolii* Price, 1973 (= nomen nudum)

- A. amsinckiae* (Steiner & Scott, 1935) Thorne, 1961  
 syn. *Anguillulina dipsaci* var. *amsinckiae* Steiner & Scott, 1935  
*Ditylenchus amsinckiae* (Steiner & Scott) Filipjev & Schuurmans Stekhoven, 1941  
*Mesoanguina amsinckiae* (Steiner & Scott) Chizhov & Subbotin, 1985
- A. australis* Steiner, 1940
- A. funesta* Price, Fisher & Kerr, 1979
- A. graminis* (Hardy, 1850) Filipjev, 1936  
 syn. *Vibrio graminis* Hardy, 1850  
*Tylenchus graminis* (Hardy) Marcinowski 1909  
*Anguillulina graminis* (Hardy) Goodey, 1932
- A. microlaenae* (Fawcett, 1938) Steiner, 1940  
 syn. *Anguillulina microlaenae* Fawcett, 1938
- A. tumefaciens* (Cobb, 1932) Filipjev & Schuurmans Stekhoven, 1941  
 syn. *Tylenchus tumefaciens* Cobb, 1932  
*Anguillulina tumefaciens* (Cobb) Goodey, 1933  
*Pratylenchus tumefaciens* (Cobb) Filipjev, 1936  
*Afrina tumefaciens* (Cobb) Brzeski, 1981  
*Subanguina tumefaciens* (Cobb) Fortuner & Maggenti, 1987
- A. wevelli* (Van den Berg, 1985) comb. n. (syn. of *A. agrostis* for Chizhov & Subbotin, 1990)  
 syn. *Afrina wevelli* Van den Berg, 1985  
*Subanguina wevelli* (Van den Berg) Ebsary, 1991

ETYMOLOGY. Feminine form of Latin *anguinus* = snake-like.

The type species was described from wheat seed-galls in Piedmont, Northern Italy. Keys to species of *Anguina*, *Subanguina*, *Heteroanguina* and *Mesoanguina* have been given by Chizhov and Subbotin (1990).

### **Genus *Subanguina* Paramonov, 1967**

syn. ***Caconema* Cobb, 1924 (= senior objective syn.)**

***Cynipanguina* Maggenti, Hart & Paxman, 1974**

***Heteroanguina* Chizhov, 1980**

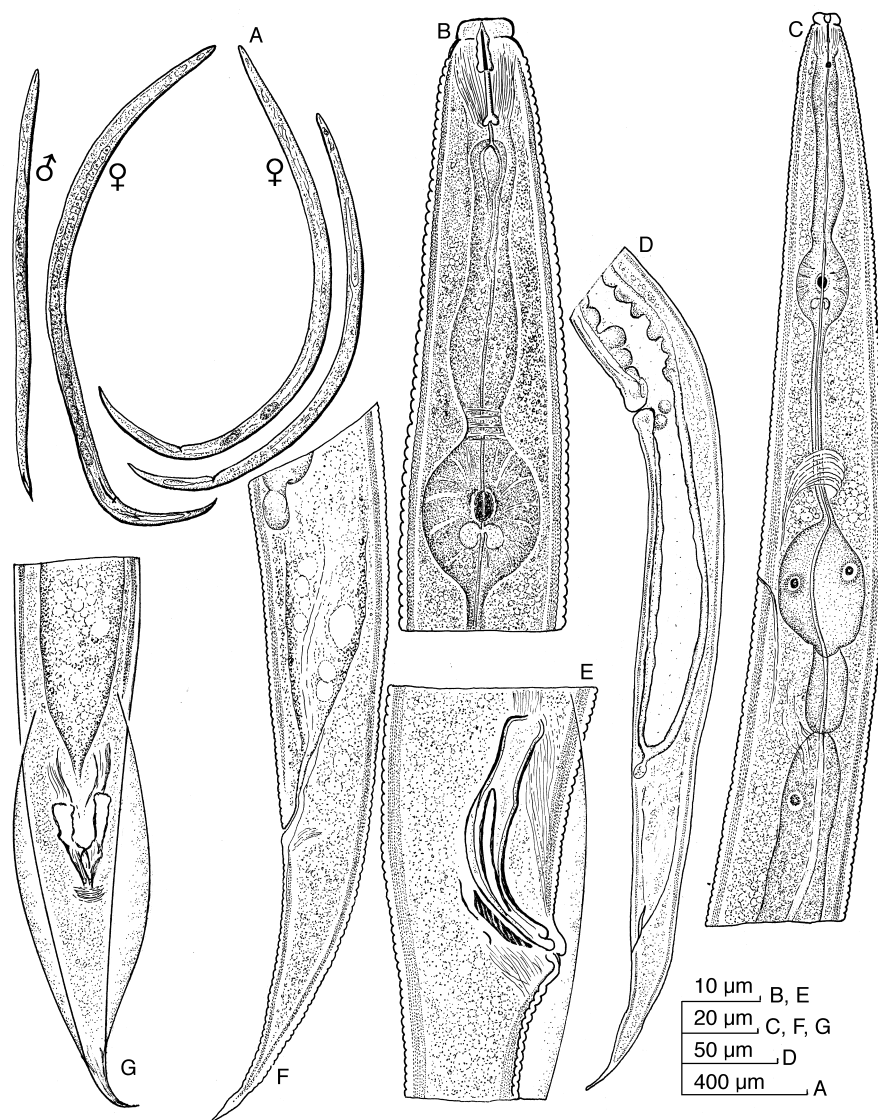
***Afrina* Brzeski, 1981**

***Mesoanguina* Chizhov & Subbotin, 1985**

(Figs 47; 49, E and F)

### **Diagnosis**

Anguininae. Medium- to large-sized (1–2 mm), **mature female** vermiform or obese, **generally not spirally coiled**. Median oesophageal bulb muscular, with refractive thickening. Basal bulb continuous with or offset from isthmus by a constriction. **Crustaformeria with four to six rows each of eight to 12 cells. Oocytes in one to two rows, not arranged about a rachis.** Ovary and testis may have one to two flexures. Bursa subterminal. Fourth-stage juvenile generally resistant and infective. Type species incites galls with well-developed internal cavity on roots of grasses; other species incite galls on stems, leaves or inflorescence.



**Fig. 47.** *Subanguina radicicola* (Greeff) from annular grass in Harpenden, England. A. Adults. B and C. Female oesophageal regions. D and F Female tail ends. E. Spicular region. G. Male tail end.

### Type species

*Subanguina radicicola* (Greeff, 1872) Paramonov, 1967

syn. *Anguillula radicicola* Greeff, 1872

*Tylenchus radicicola* (Greeff) Örley, 1880

*Heterodera radicicola* (Greeff) Müller, 1884

*Heterobolbus radicicola* (Greeff) Julien, 1898

*Caconema radicicola* (Greeff) Cobb, 1924

*Anguillulina radicola* (Greeff) Goodey, 1932  
*Ditylenchus radicola* (Greeff) Filipjev, 1936  
*Anguina radicola* (Greeff) Teploukhova, 1967  
*Tylenchus hordei* Schøyen, 1885  
*Subanguina hordei* (Schøyen) Siddiqi, 1986

#### Other species

- Subanguina askenasyi* (Bütschli, 1873) Brzeski, 1981  
 syn. *Tylenchus askenasyi* Bütschli, 1873  
*Anguillulina askenasyi* (Bütschli) Steiner, 1936  
*Ditylenchus askenasyi* (Bütschli) Goodey, 1951  
*Anguina askenasyi* (Bütschli) Krall, 1971
- S. balsamophila* (Thorne, 1926) comb. n.  
 syn. *Tylenchus balsamophilus* Thorne, 1926  
*Anguillulina balsamophila* (Thorne) Goodey, 1932  
*Anguina balsamophila* (Thorne) Filipjev, 1936  
*Ditylenchus balsamophilus* (Thorne) Filipjev & Schuurmans Stekhoven, 1941  
*Mesoanguina balsamophila* (Thorne) Chizhov & Subbotin, 1985
- S. brenani* (Goodey, 1945) Brzeski, 1981  
 syn. *Anguillulina brenani* Goodey, 1945  
*Ditylenchus brenani* (Goodey) Goodey, 1951  
*Anguina brenani* (Goodey) Kirjanova & Krall, 1971
- S. caricis* (Solovyeva & Krall, 1982) comb. n.  
 syn. *Anguina caricis* Solovyeva & Krall, 1982  
*Heteroanguina caricis* (Solovyeva & Krall) Chizhov & Subbotin, 1985
- S. centaureae* (Kirjanova & Ivanova, 1969) Brzeski, 1981  
 syn. *Paranguina centaureae* Kirjanova & Ivanova, 1969  
*Mesoanguina centaureae* (Kirjanova & Ivanova) Chizhov & Subbotin, 1985
- S. chartolepidis* (Poghossian, 1966) Brzeski, 1981  
 syn. *Anguina chartolepidis* Poghossian, 1966  
*Mesoanguina chartolepidis* (Poghossian) Chizhov & Subbotin, 1985
- S. chrysopogoni* Bajaj, Dabur, Pruthi & Bhatti, 1990
- S. cousiniae* (Kirjanova & Ivanova) Brzeski, 1981  
 syn. *Paranguina cousiniae* Kirjanova & Ivanova, 1969  
*Mesoanguina cousiniae* (Kirjanova & Ivanova) Chizhov & Subbotin, 1985
- S. danthoniae* (Maggenti, Hart & Paxman, 1974) comb. n.  
 syn. *Cynipanguina danthoniae* Maggenti, Hart & Paxman, 1974  
*Anguina danthoniae* (Maggenti *et al.*) Brzeski, 1981
- S. ferulae* (Ivanova, 1977) Brzeski, 1981  
 syn. *Anguina ferulae* Ivanova, 1977  
*Heteroanguina ferulae* (Ivanova) Chizhov & Subbotin, 1985
- S. graminophila* (Goodey, 1933) Brzeski, 1981  
 syn. *Anguillulina graminophila* Goodey, 1933  
*Ditylenchus graminophilus* (Goodey) Filipjev, 1936  
*Pratylenchus graminophilus* (Goodey) Filipjev, 1936  
*Anguina graminophila* (Goodey) Thorne, 1961

- Heteroanguina graminophila* (Goodey) Chizhov, 1980  
*Anguina calamagrostis* Wu, 1967  
*S. calamagrostis* (Wu) Brzeski, 1981
- S. guizotiae* (Van den Berg, 1986) Ebsary, 1991  
 syn. *Anguina guizotiae* Van den Berg, 1986  
*Mesoanguina guizotiae* (Van den Berg) Chizhov & Subbotin, 1990
- S. hyparrheniae* (Corbett, 1966) Fortuner & Maggenti, 1987  
 syn. *Anguina hyparrheniae* Corbett, 1966  
*Afrina hyparrheniae* (Corbett) Brzeski, 1981
- S. klebahni* (Goffart, 1942) Siddiqi, 1986  
 syn. *Anguina klebahni* Goffart, 1942
- S. kopetdaghica* (Kirjanova & Shagalina, 1969) Brzeski, 1981  
 syn. *Anguina kopetdaghica* Kirjanova & Shagalina, 1969  
*Mesoanguina kopetdaghica* (Kirjanova & Shagalina) Chizhov & Subbotin, 1985
- S. millefolii* (L  w, 1874) Brzeski, 1981  
 syn. *Tylenchus millefolii* L  w, 1874  
*Anguillulina millefolii* (L  w) Goodey, 1932  
*Anguina millefolii* (L  w) Filipjev, 1936  
*Mesoanguina millefolii* (L  w) Chizhov & Subbotin, 1985
- S. mobilis* (Chit & Fisher, 1975) Brzeski, 1981  
 syn. *Anguina mobilis* Chit & Fisher, 1975  
*Mesoanguina mobilis* (Chit & Fisher) Chizhov & Subbotin, 1985
- S. montana* (Kirjanova & Ivanova, 1969) Brzeski, 1981  
 syn. *Paranguina montana* Kirjanova & Ivanova, 1969  
*Mesoanguina montana* (Kirjanova & Ivanova) Chizhov & Subbotin, 1985
- S. moxae* (Yokoo & Choi, 1968) Brzeski, 1981  
 syn. *Anguina moxae* Yokoo & Choi, 1968  
*Mesoanguina moxae* (Yokoo & Choi) Chizhov & Subbotin, 1985
- S. pharangii* (Chizhov, 1984) Siddiqi, 1986  
 syn. *Anguina pharangii* Chizhov, 1984  
*Mesoanguina pharangii* (Chizhov) Chizhov & Subbotin, 1985
- S. picridis* (Kirjanova, 1944) Brzeski, 1981  
 syn. *Anguillulina picridis* Kirjanova, 1944  
*Anguina picridis* (Kirjanova) Kirjanova, 1957  
*Paranguina picridis* (Kirjanova) Kirjanova & Ivanova, 1969  
*Mesoanguina picridis* (Kirjanova) Chizhov & Subbotin, 1985
- S. plantaginis* (Hirschmann, 1978) Brzeski, 1981  
 syn. *Anguina plantaginis* Hirschmann, 1978  
*Mesoanguina plantaginis* (Hirschmann) Chizhov & Subbotin, 1985
- S. polygoni* (Poghossian, 1966) Brzeski, 1981  
 syn. *Anguina polygoni* Poghossian, 1966  
*Heteroanguina polygoni* (Poghossian) Chizhov & Subbotin, 1985
- S. pustulicola* (Thorne, 1934) Siddiqi, 1986  
 syn. *Anguillulina pustulicola* Thorne, 1934  
*Ditylenchus pustulicola* (Thorne) Filipjev & Schuurmans Stekhoven, 1941  
*Anguina pustulicola* (Thorne) Goodey, 1951
- S. spermophaga* (Steiner, 1937) Siddiqi, 1986



- syn. *Anguina spermophaga* Steiner, 1937  
*S. tridomina* (Kirjanova, 1958) Siddiqi, 1986  
 syn. *Anguina tridomina* Kirjanova, 1958 (? syn. of *S. graminophila*)  
*S. varsobica* (Kirjanova & Ivanova, 1969) Brzeski, 1981  
 syn. *Paranguina varsobica* Kirjanova & Ivanova, 1969  
*Mesoanguina varsobica* (Kirjanova & Ivanova) Chizhov & Subbotin, 1985

## Remarks

Andrássy (*in litt.*) has pointed out to me that the genus *Caconema* Cobb, 1924, was proposed to accommodate the species *C. radiculicola* (Greeff, 1872), which is the type species of *Subanguina* Paramonov, 1967. Thus *Caconema* becomes a senior objective synonym of *Subanguina* and must replace the latter name. As discussed under the genus *Meloidogyne*, Cobb (1924) proposed the genus *Caconema* for *Heterodera radiculicola* (Greeff) Müller as type species. Cobb had misidentified the type species because he illustrated and described a *Meloidogyne* sp. (see discussion under *Meloidogyne*). Tarjan & Hopper (1974) stated that 'Müller (1884) erroneously assumed that he and Greeff worked with the same species. His combination and Cobb's actually apply to *Anguillula marioni* Cornu, 1879.' *Caconema* was later synonymized with *Meloidogyne* and that action was accepted by many taxonomists. Siddiqi (1986) listed the genus as a synonym of *Meloidogyne*, whereas its type species was listed as a synonym of *Subanguina radiculicola*!

The position of *Caconema* as a senior synonym of *Subanguina* cannot be disputed since both are based on the same type species. However, it is clear that *Caconema* is based on a misidentified species and, following ICZN Article 67 (i) and Article 70 (b), the case should be referred to the Commission for a ruling. The case is made out more strongly for suppressing the senior objective synonym *Caconema* on the grounds that this name has not been used as a valid name during the immediately preceding 50 years and that the junior objective synonym *Subanguina* has been used as valid name by more than five authors and in more than ten publications during the same period (as required by Article 79 (c) (1 and 2)). An application has to be made to the ICZN for the suppression of an unused senior objective synonym and to preserve the junior synonym *Subanguina* for the sake of stability in taxonomy. Until such a ruling is obtained, *Caconema* is considered as an invalid senior synonym of *Subanguina*.

*Cynipanguina* has been differentiated from *Anguina* by having a digit-like basal extension of the oesophagus and only adults as the resistant stage. A somewhat similar extension is sometimes seen in *Subanguina radiculicola*. Adults of *S. radiculicola* are also the resistant stage (Chizhov & Mar'enko, 1984). Hence *Cynipanguina* cannot be differentiated from *Subanguina* and becomes its junior synonym. The digit-like oesophageal extension seen in *Cynipanguina* is a continuation of the oesophageal glands and is not similar to that found in the free-living forms of the superfamily Sphaerularioidea.

ETYMOLOGY. From Latin *sub* = under, and *Anguina*.

The type species was found within root-galls of meadow grass (*Poa annua*) and couch grass (*Agropyron repens*) in Germany. It is widely distributed in Europe.

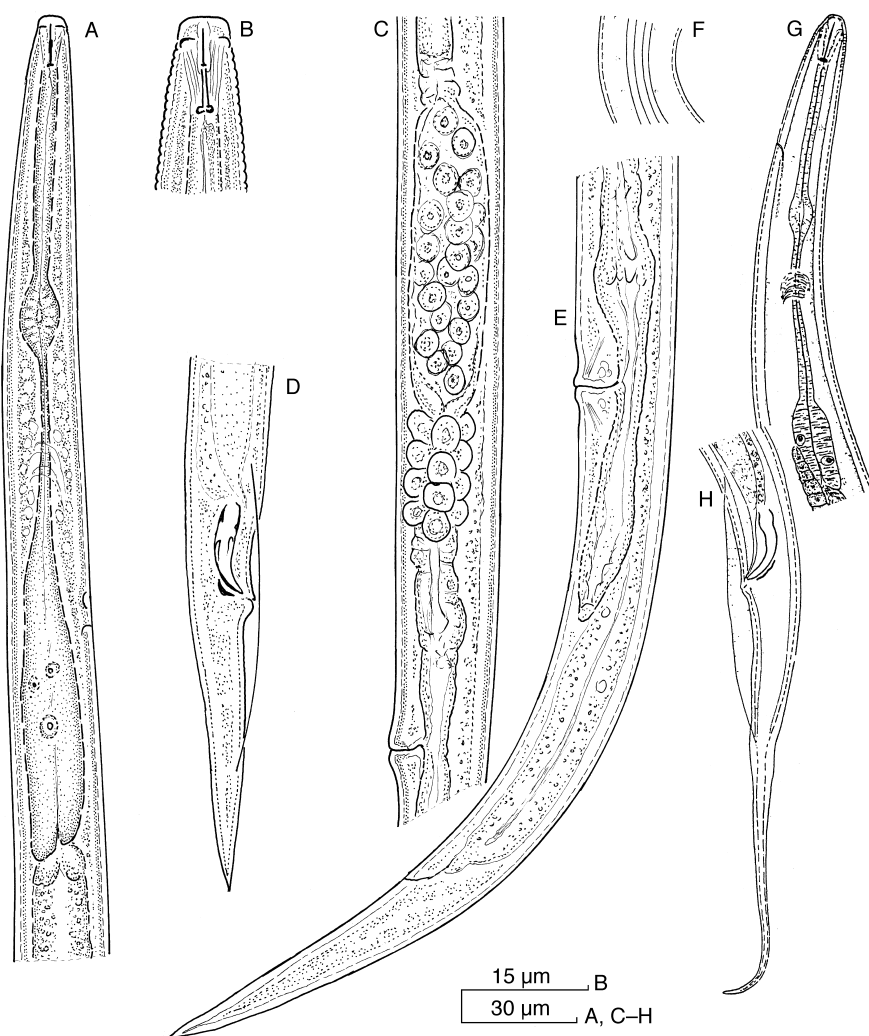
**Genus *Ditylenchus* Filipjev, 1936**syn. *Anguillulina* (*Ditylenchus* Filipjev) (Schneider, 1939)(*Ditylenchus* Filipjev, 1934 = *nomen nudum*)

(Figs 48, A–E; 49, A and B)

**Diagnosis**

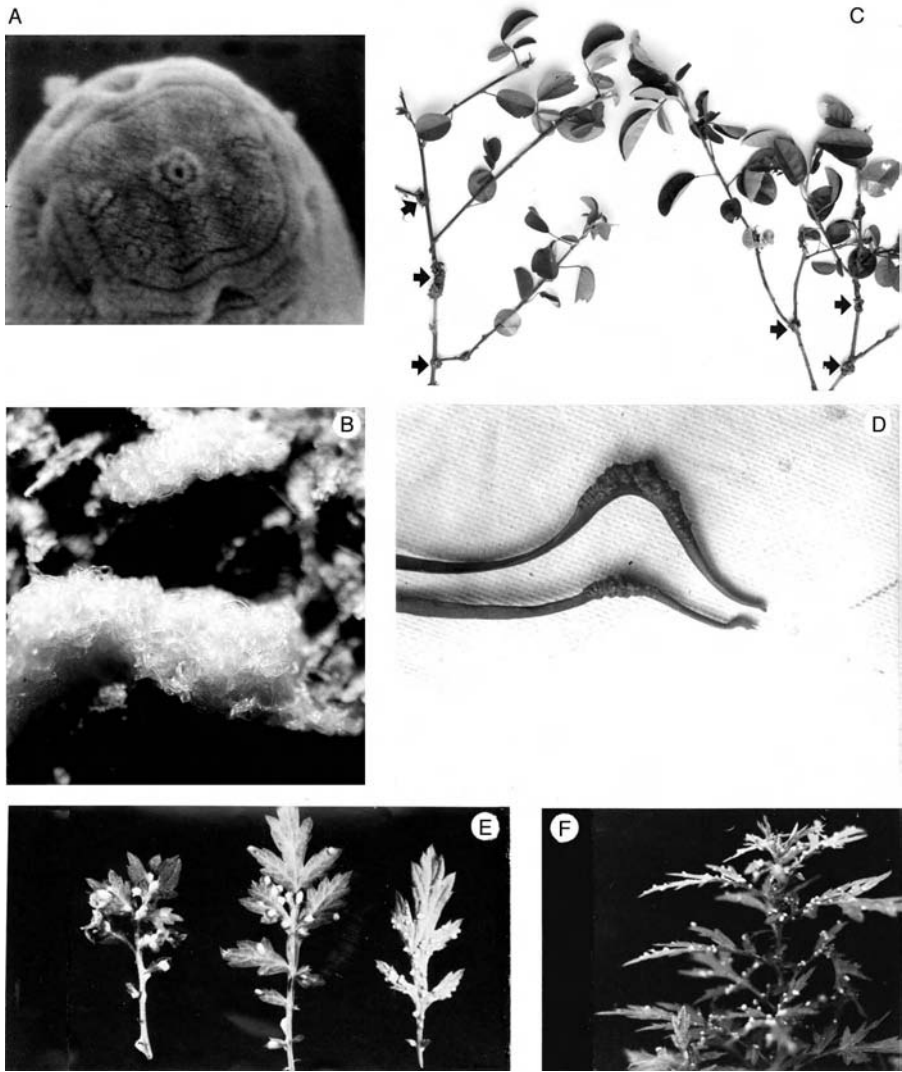
Anguininae. Body usually under 1.5 mm long, not curving strongly when relaxed; **mature adults slender**. Lateral field with four or six (occasionally more) incisures, which may be indistinct. Median bulb muscular or non-muscular, with or without refractive thickenings. Isthmus not marked off from basal bulb. **Basal bulb a thin elastic sac containing oesophageal glands**; base of bulb may extend over intestine but the nuclei of glands remain within the bulb anterior to oesophago-intestinal junction. Intestine with two normal-sized but often hyaline cells at its anterior end, possibly acting as a valve; lumen of intestine not considerably narrowed in anterior region. **Ovary outstretched, with one or two rows of oocytes. Crustaformeria in form of a quadricolumella of four rows of four cells each**. Spermatheca elongate axial sac. Vagina at right angle to body axis or nearly so, not directed forward. **Postvulval uterine sac present**. Testis outstretched. Bursa adanal to subterminal, never enclosing tail tip. Tails elongate-conoid to subcylindrical or filiform. Fungal feeders and parasites of higher plants, several species, including the type species, are capable of attacking aerial parts.

**Type species***Ditylenchus dipsaci* (Kühn, 1857) Filipjev, 1936syn. *Anguillula dipsaci* Kühn, 1857*Anguillulina dipsaci* (Kühn) Gervais & Van Beneden, 1859*Tylenchus dipsaci* (Kühn) Bastian, 1865*Anguillulina dipsaci* var. *allocotus* Steiner, 1934*Ditylenchus allocotus* (Steiner) Filipjev & Schuurmans Stekhoven, 1941*Anguillulina dipsaci* var. *communis* Steiner & Scott, 1935*Ditylenchus dipsaci* var. *narcissi* de Bruyn Ouboter, 1930*Anguillula devastatrix* Kühn, 1869*Tylenchus devastatrix* (Kühn) Örley, 1880*Anguillulina devastatrix* (Kühn) Neveu-Lemaire, 1913*Ditylenchus devastatrix* (Kühn) Tarjan, 1960 (wrongly attributed to Filipjev & Schuurmans Stekhoven, 1941 by Tarjan, 1960)*Anguillula secalis* Nitschke, 1868*Anguillulina secalis* (Nitschke) Goodey, 1932*Ditylenchus secalis* (Nitschke) Siddiqi, 1986*Tylenchus allii* Beijerinck, 1883*Ditylenchus allii* (Beijerinck) Tarjan, 1960 (wrongly attributed to Filipjev & Schuurmans Stekhoven, 1941 by Tarjan, 1960)*Tylenchus havensteinii* Kühn, 1881*Anguillulina havensteinii* (Kühn) Goodey, 1932*Ditylenchus havensteinii* (Kühn) Siddiqi, 1986*Tylenchus hyacinthi* Prillieux, 1881*Anguillulina hyacinthi* (Prillieux) Goodey, 1932



**Fig. 48.** A–E. *Ditylenchus dipsaci* (Kühn) from Sweden. F–H. *Indoditylenchus sundarbanensis* Sinha, Choudhury & Baqri. A and G. Oesophageal region of female and male, respectively. B. Head end of female. C. Vulva–spermatheca region. D and H. Tail ends of males. E. Posterior region of female. F. Lateral field at midbody of male. (F–H. After Sinha *et al.*, 1991.)

(syn.) *Ditylenchus hyacinthi* (Prillieux) Filipjev & Schuurmans Stekhoven, 1941  
*Tylenchus putrefaciens* Kühn, 1879  
*Anguillulina putrefaciens* (Kühn) Braun, 1895  
*Ditylenchus putrefaciens* (Kühn) Tarjan, 1967 (wrongly attributed to Filipjev  
 & Schuurmans Stekhoven, 1941 by Tarjan, 1967)



**Fig. 49.** A. Scanning electron micrograph of *en face* view of head of *Ditylenchus dipsaci* (Kühn). B. 'Eelworm wool' of *D. dipsaci*. C. Stem-galls of *Desmodium ovalifolium* caused by *Pterotylenchus cecidogenus* Siddiqi & Lenné in Colombia. D. Galls on *Ascophyllum nodosum* (seaweed) from Irish coast caused by *Halenchus fucicola* (de Man & Barton). E and F. Leaf-galls of *Artemisia asiatica* caused by *Subanguina moxae* (Yokoo & Choi) in Korea. (A. Courtesy R.W. McLeod. C. After Siddiqi and Lenné (1984). D. Courtesy R.G. Davide. E and F. After Choi and Loof (1974), courtesy *Nematologica*.)

- Ditylenchus dipsaci falcariae* Poghossian, 1967  
*Ditylenchus fragariae* Kirjanova, 1951  
*Tylenchus dipsaci* var. *tobaensis* Schneider, 1937  
*Ditylenchus dipsaci* var. *tobaensis* (Schneider) Kirjanova, 1951  
*Ditylenchus tobaensis* (Schneider) Kirjanova, 1951  
*Ditylenchus phloxidis* Kirjanova, 1951  
*Ditylenchus sonchophila* Kirjanova in Paramonov, 1970  
*Ditylenchus galeopsidis* Teploukhova in Paramonov, 1970

#### Other species

- Ditylenchus acutatus* Brzeski, 1991  
*D. africanus* Wendt, Swart, Vrain & Webster, 1995  
*D. angustus* (Butler, 1913) Filipjev, 1936  
 syn. *Tylenchus angustus* Butler, 1913  
*Anguillulina angusta* (Butler) Goodey, 1932  
*D. ausafi* Husain & Khan, 1967  
*D. australiae* Brzeski, 1984  
*D. beljaevae* Karimova, 1957  
*D. brevicauda* (Micoletzky, 1925) Filipjev, 1936  
 syn. *Tylenchus brevicauda* Micoletzky, 1925, nec *Tylenchus coffeae brevicauda* Rahm, 1928  
*Anguillulina brevicauda* (Micoletzky) Goodey, 1932  
*D. caudatus* Thorne & Malek, 1968  
*D. clarus* Thorne & Malek, 1968  
*D. convallariae* Sturhan & Friedman, 1965  
*D. cyperi* Husain & Khan 1967  
*D. daumiae* Brzeski & Palmisano, 1990  
*D. deiridus* Thorne & Malek, 1968  
*D. destructor* Thorne, 1945  
*D. dipsacoideus* (Andrássy, 1952) Andrásy, 1956  
 syn. *Anguillulina (Ditylenchus) dipsacoidea* Andrásy, 1952  
*D. drepanocercus* Goodey, 1953  
*D. dryadis* Anderson & Mulvey, 1980  
*D. elegans* Zell, 1988  
*D. emus* Khan, Chawla & Prasad, 1969  
*D. equalis* Heyns, 1964  
*D. exilis* Brzeski, 1984  
*D. filenchulus* Brzeski, 1991  
*D. filicauda* Geraert & Raski, 1990  
*D. filimus* Anderson, 1983  
*D. flagellicauda* Geraert & Raski, 1990  
*D. geraerti* (Paramonov, 1970) Bello & Geraert in Bello, 1971  
 syn. *Tylenchus geraerti* Paramonov, 1970  
*Ditylenchus procerus* apud Geraert, 1962  
*D. humili* Skarbilovich, 1972  
*D. inobservabilis* (Kirjanova, 1938) Kirjanova, 1961  
 syn. *Anguillulina inobservabilis* Kirjanova, 1938

- D. intermedius* (de Man, 1880) Filipjev, 1936  
 syn. *Tylenchus intermedius* de Man, 1880  
*Anguillulina intermedia* (de Man) Goodey, 1932  
*D. istatae* Samibaeva, 1966  
*D. leptosoma* Geraert & Choi, 1990  
*D. longicauda* Choi & Geraert, 1988  
*D. longimatrixalis* (Kazachenko, 1975) Brzeski, 1984  
 syn. *Basiroides longimatrixalis* Kazachenko, 1975  
*Basiria longimatrixalis* (Kazachenko) Bajaj and Bhatti in Fortuner, 1985  
*Basiria leptolongimatrixalis* Bajaj & Bhatti, 1979 (a wrong spelling of *longimatrixalis*)  
*D. medicaginis* Wasilewska, 1965  
*D. melongena* Bhatnagar & Kadyan, 1969  
*D. microdens* Thorne & Malek, 1968 (syn. of *D. equalis* for Brzeski, 1998)  
*D. minutus* Husain & Khan, 1967  
*D. mirus* Siddiqi, 1963  
*D. myceliophagus* Goodey, 1958  
*D. nanus* Siddiqi, 1963  
*D. nortoni* (Elmiligy, 1971) Bello & Geraert, 1972 (syn. of *D. equalis* for Brzeski, 1998)  
 syn. *Basiroides nortoni* Elmiligy, 1971, nec *Basiroides nortoni* (Thorne & Malek, 1968) Fotedar & Mahajan, 1973 (= *Basiria nortoni* Thorne & Malek, 1968)  
*D. obesus* Thorne & Malek, 1968  
*D. parcevivens* Andr  ssy, 1998  
*D. parvus* Zell, 1988  
*D. procerus* (Bally & Reydon, 1931) Filipjev, 1936  
 syn. *Tylenchus procerus* Bally & Reydon, 1931  
*Anguillulina procera* (Bally & Reydon) Goodey, 1932  
*D. sibiricus* German, 1969 (syn. of *D. equalis* for Brzeski, 1991)  
*D. silvaticus* Brzeski, 1991  
*D. solani* Husain & Khan, 1976  
*D. sorghii* Verma, 1966  
*D. taleolus* (Kirjanova, 1938) Kirjanova, 1961  
 syn. *Anguillulina taleola* Kirjanova, 1938  
*D. tausaghyzatus* (Kirjanova, 1938) Kirjanova, 1961  
 syn. *Anguillulina tausaghyzata* Kirjanova, 1938  
*D. tenuidens* Gritsenko, 1971  
*D. terricola* Brzeski, 1991 (spelling emended from *terricolus*)  
*D. triformis* Hirschmann & Sasser, 1955  
*D. valveus* Thorne & Malek, 1968  
*D. virtudesae* Tobar Jim  nez, 1964

#### Species inquirendae

- Ditylenchus cafeicola* (Schuurmans Stekhoven, 1951) Andr  ssy, 1954  
 syn. *Tylenchus cafeicola* Schuurmans Stekhoven, 1951  
*D. darbouxi* (Cotte, 1912) Filipjev, 1936

- syn. *Tylenchus darbouxi* Cotte, 1912  
*Anguillulina darbouxi* (Cotte) Goodey, 1932  
*D. karakalpakensis* Erzhanov, 1964  
*D. pumilus* Karimova, 1957  
*D. sycobius* (Cotte, 1920) Filipjev, 1936  
 syn. *Tylenchus sycobius* Cotte, 1920  
*Anguillulina sycobia* (Cotte) Goodey, 1932  
*D. tenuis* (Kischke, 1956) Brzeski, 1991  
 syn. *Tylenchus davainei* var. *tenuis* Kischke, 1956, nec *Tylenchus tenuis* Micoletzky, 1922  
*Tylenchus kischkei* Meyl, 1961  
*D. kischkeae* (Meyl, 1961) Loof, 1985  
*D. tulaganovi* Karimova, 1957

#### Species incertae sedis

- Ditylenchus bacillifer* (Micoletzky, 1922) Filipjev, 1936  
 syn. *Tylenchus bacillifer* Micoletzky, 1922  
*Anguillulina bacillifer* (Micoletzky) Goodey, 1932 (? = *Deladenus*)  
*D. brassicae* Husain & Khan, 1976 (The shapes of the spermatheca and sperm exclude it from Anguinidae. It appears to belong to *Filenchus*.)  
*D. sapari* Atakhanov, 1958 (? = *Neoditylenchus*)

ETYMOLOGY. From first two letters of type species name *dipsaci*, and *Tylenchus*.

The type species was described from Fuller's teasel, *Dipsacus fullonum*, in Germany. It attacks over 450 plant species and occurs in biological races or biotypes. A computerized key to *Ditylenchus* spp. is given by Viscardi and Brzeski (1993).

#### Genus *Nothotylenchus* Thorne, 1941

syn. *Boleodoroides* Mathur, Khan & Prasad, 1966

*Boleodorus* (*Boleodoroides* Mathur *et al.*, 1966) (Khera, 1970)

(Fig. 53, J and K)

#### Diagnosis

Anguininae. Body generally 0.5–1.2 mm long. Cuticle finely striated; lateral field with four or six incisures, rarely a plain band. Cephalic framework of six equal sectors, not sclerotized. Stylet 5–12  $\mu\text{m}$  long, with conus less than half its total length, knobs rounded. Orifice of dorsal oesophageal gland usually 1.5–3  $\mu\text{m}$  from stylet base. **Median oesophageal bulb non-muscular, non-valvate, not assisting in active feeding. Oesophageal glands enclosed in a basal bulb** of variable shape and size, offset from intestine or base sometimes lobed. Vulva at 65–85% of body length. Postvulval uterine sac one body width or more long. Spermatheca elongate-axial. Tail elongate-conoid, rarely filiform, tip pointed or narrowly rounded. Bursa arising near head of spicules and generally extending to middle of tail, rarely adanal, **never terminal**.

## Type species

*Nothotylenchus acris* Thorne, 1941

syn. *Ditylenchus acris* (Thorne) Fortuner & Maggenti, 1987

## Other species

*Nothotylenchus acutus* Khan, 1965

syn. *Ditylenchus acutus* (Khan, 1965) Fortuner & Maggenti, 1987

*Nothotylenchus allii* Khan & Siddiqi, 1968

*Ditylenchus alliphilus* Fortuner & Maggenti, 1987 (was a nom. nov. for *Ditylenchus allii* (Khan & Siddiqi, 1968), nec *D. allii* (Beijerinck, 1883) Filipjev & Schuurmans Stekhoven, 1941)

*Nothotylenchus srinagarensis* Fotedar & Mahajan, 1974

*Ditylenchus srinagarensis* (Fotedar & Mahajan) Fortuner & Maggenti, 1987

*Nothotylenchus indicus* Saxena, Chhabra & Joshi, 1973

*Ditylenchus indicus* (Saxena, Chhabra & Joshi) Fortuner & Maggenti, 1987

*Ditylenchus saxenai* Fortuner & Maggenti, 1987 (= objective syn., was a nom. nov. for *Ditylenchus indicus* Saxena, Chhabra & Joshi, 1973, nec *D. indicus* (Sethi & Swarup, 1967) Fortuner, 1982, now *Safianema indicum*)

*N. adasi* Sykes, 1980

syn. *Ditylenchus adasi* (Sykes, 1980) Fortuner & Maggenti, 1987

*N. affinis* Thorne, 1941

syn. *Ditylenchus affinis* (Thorne) Fortuner & Maggenti, 1987

*N. antricolus* Andr  ssy, 1961

syn. *Ditylenchus antricolus* (Andr  ssy) Fortuner & Maggenti, 1987

*N. attenuatus* Mulvey, 1969

syn. *Ditylenchus attenuatus* (Mulvey) Fortuner & Maggenti, 1987

*N. atypicus* (Khera & Chaturvedi, 1977) Siddiqi, 1986

syn. *Boleodorus atypicus* Khera & Chaturvedi, 1977

*Ditylenchus atypicus* (Khera & Chaturvedi) Fortuner & Maggenti, 1987

*N. basiri* Khan, 1965

syn. *Ditylenchus basiri* (Khan) Fortuner & Maggenti, 1987

*N. bhatnagari* Tikyani & Khera, 1969

syn. *Ditylenchus bhatnagari* (Tikyani & Khera) Fortuner & Maggenti, 1987

*N. boroki* Gagarin, 1999

*N. buckleyi* Das, 1960

syn. *Ditylenchus buckleyi* (Das) Fortuner & Maggenti, 1987

*N. citri* (Varaprasad, Khan & Lal, 1981) Siddiqi, 1986

syn. *Paurodontus citri* Varaprasad, Khan & Lal, 1981

*Ditylenchus citri* (Varaprasad, Khan & Lal) Fortuner & Maggenti, 1987

*N. clavatus* Dhanachand & Gambhir, 1991

*N. compactus* Massey, 1974

syn. *Ditylenchus compactus* (Massey) Fortuner & Maggenti, 1987

*N. cylindricollis* Thorne, 1941

syn. *Ditylenchus cylindricollis* (Thorne) Fortuner & Maggenti, 1987

*N. cylindricus* Khan & Siddiqi, 1968

syn. *Ditylenchus cylindricus* (Khan & Siddiqi) Fortuner & Maggenti, 1987

*Nothotylenchus elongatus* Husain & Khan, 1974



- Ditylenchus elongatus* (Husain & Khan) Siddiqi, 1986  
*Ditylenchus elongatus* (Husain & Khan) Fortuner & Maggenti, 1987
- N. danubialis* Andr  ssy, 1960  
 syn. *Ditylenchus danubialis* (Andr  ssy) Fortuner & Maggenti, 1987
- N. drymocolus* R  hm, 1956  
 syn. *Ditylenchus drymocolus* (R  hm) Brzeski, 1991
- N. exiguus* Andr  ssy, 1958  
 syn. *Ditylenchus exiguus* (Andr  ssy) Fortuner & Maggenti, 1987
- N. ferepolitor* Kazachenko, 1980  
 syn. *Ditylenchus ferepolitor* (Kazachenko, 1980) Fortuner & Maggenti, 1987  
*N. silvestris* Kazachenko, 1980 (syn. by Brzeski, 1998)  
*Ditylenchus silvestris* (Kazachenko, 1980) Fortuner & Maggenti, 1987  
*Ditylenchus protensus* Brzeski, 1984 (syn. by Brzeski, 1998)  
*N. protensus* (Brzeski) comb. n.
- N. fotedari* Mahajan, 1977  
 syn. *Ditylenchus fotedari* (Mahajan) Fortuner & Maggenti, 1987
- N. geraerti* Kheiri, 1971  
 syn. *Ditylenchus kheirii* Fortuner & Maggenti, 1987 (was a nom. nov. for  
*Ditylenchus geraerti* (Kheiri, 1971) Fortuner & Maggenti, 1987, nec *D.*  
*geraerti* (Paramonov, 1970) Bello & Geraert in Bello, 1971)
- N. goldeni* Maqbool, 1982  
 syn. *Ditylenchus goldeni* (Maqbool) Fortuner & Maggenti, 1987
- N. hexaglyphus* Khan & Siddiqi, 1968  
 syn. *Ditylenchus hexaglyphus* (Khan & Siddiqi) Fortuner & Maggenti, 1987
- N. loksai* Andr  ssy, 1959  
 syn. *Ditylenchus loksai* (Andr  ssy) Fortuner & Maggenti, 1987
- N. longistylus* (Khera & Chaturvedi, 1977) Siddiqi, 1986  
 syn. *Boleodor longistylus* Khera & Chaturvedi, 1977  
*Ditylenchus longistylus* (Khera & Chaturvedi) Fortuner & Maggenti, 1987
- N. major* Thorne & Malek, 1968  
 syn. *Ditylenchus maleki* Fortuner & Maggenti, 1987 (= junior objective syn.)  
*Ditylenchus major* (Thorne & Malek) Brzeski, 1991
- N. medians* Thorne & Malek, 1968  
 syn. *Ditylenchus medians* (Thorne & Malek) Fortuner & Maggenti, 1987
- N. montanus* Kiknadze & Eliashvilli, 1988  
 syn. *Ditylenchus montanus* (Kiknadze & Eliashvilli) Brzeski, 1991
- N. oryzae* (Mathur, Khan & Prasad, 1966) Siddiqi, 1986  
 syn. *Boleodoroides oryzae* Mathur, Khan & Prasad, 1966  
*Paurodontus oryzae* (Mathur, Khan & Prasad) Sumenkova, 1975  
*Ditylenchus oryzae* (Mathur, Khan & Prasad) Fortuner & Maggenti, 1987
- N. paramonovi* Gagarin, 1974  
 syn. *Ditylenchus paramonovi* (Gagarin) Fortuner & Maggenti, 1987
- N. parasimilis* Massey, 1974  
 syn. *Ditylenchus parasimilis* (Massey) Fortuner & Maggenti, 1987
- N. petilus* Massey, 1974  
 syn. *Ditylenchus petilus* (Massey) Fortuner & Maggenti, 1987
- N. similis* Thorne & Malek, 1968

- syn. *Ditylenchus similis* (Thorne & Malek) Fortuner & Maggenti, 1987  
*N. singhi* Das & Shivaswamy, 1980  
 syn. *Ditylenchus singhi* (Das & Shivaswamy) Fortuner & Maggenti, 1987  
*N. solani* (Varaprasad, Khan & Lal, 1981) Siddiqi, 1986  
 syn. *Paurodontus solani* Varaprasad, Khan & Lal, 1981  
*Ditylenchus varaprasadi* Fortuner & Maggenti, 1987 (was a nom. nov.)  
*Ditylenchus solani* (Varaprasad, Khan & Lal) Fortuner & Maggenti, 1987, nec  
*D. solani* Husain & Khan, 1976  
*N. taylori* Husain & Khan, 1974  
 syn. *Ditylenchus taylori* (Husain & Khan) Fortuner & Maggenti, 1987  
*N. tenuis* Gagarin, 1999  
*N. thornei* Andr  ssy, 1958  
 syn. *Ditylenchus thornei* (Andr  ssy) Fortuner & Maggenti, 1987  
*N. truncatus* Eliashvili & Vacheishvili, 1980  
 syn. *Ditylenchus truncatus* (Eliashvili & Vacheishvili) Fortuner & Maggenti, 1987  
*N. tuberosus* Kheiri, 1971  
 syn. *Ditylenchus tuberosus* (Kheiri) Fortuner & Maggenti, 1987  
*N. turfus* (Yokoo, 1968) Siddiqi, 1986  
 syn. *Neotylenchus turfus* Yokoo, 1968  
*Ditylenchus turfus* (Yokoo) Fortuner & Maggenti, 1987  
*N. typicus* (Husain & Khan, 1968) Siddiqi, 1986  
 syn. *Boleodorus typicus* Husain & Khan, 1968  
*N. uniformis* Truskova & Eroshenko, 1977  
 syn. *Ditylenchus uniformis* (Truskova & Eroshenko) Fortuner & Maggenti, 1987  
*N. utschini* Gagarin, 1974  
 syn. *Ditylenchus utschini* (Gagarin) Fortuner & Maggenti, 1987  
*N. websteri* Kumar, 1983  
 syn. *Ditylenchus websteri* (Kumar) Brzeski, 1991

#### Nomina nuda

- Nothotylenchus callidus* Izatullaeva, 1967  
 syn. *Ditylenchus callidus* (Izatullaeva) Fortuner & Maggenti, 1987  
*N. strictus* Kapoor, 1982

#### Species incerta sedis

- Neotylenchus nitidus* Massey, 1969  
 syn. *Nothotylenchus nitidus* (Massey, 1969) Siddiqi, 1986

ETYMOLOGY. Greek *nothos* = false, and *Tylenchus*.

The type species was found in soil about alfalfa crowns, red clover roots and sugar-beet in the USA. It is a plant-parasitic species and has been associated with strawberry disease in Japan (Nishizawa & Iyatomi, 1955).

**Genus *Safianema* Siddiqi, 1980**

(Fig. 50)

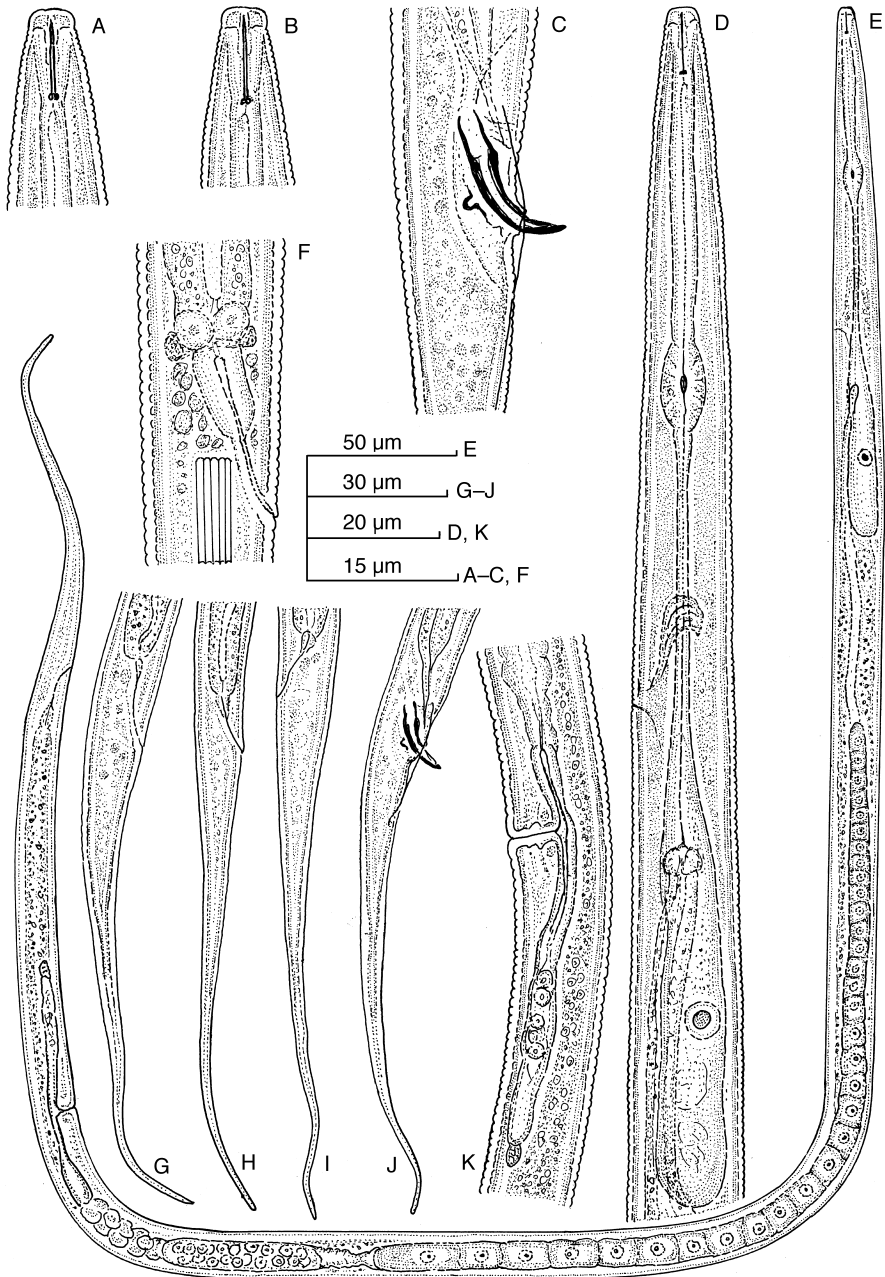
**Diagnosis**

Anguininae. Small to medium-sized (about 1 mm or less long), slender. **Six incisures in lateral field**, deirids present. Median oesophageal bulb muscular, with refractive thickenings. **Oesophageal glands overlapping anterior end of intestine**, mostly laterally, with dorsal gland being the largest and **having nucleus posterior to oesophago-intestinal junction** (early-stage juvenile may have oesophageal glands forming a bulb, suggesting that the immediate ancestor of *Safianema* had glands enclosed in a bulb). **Two anteriormost cells of the intestine modified to form a small, compact valvular structure**. **Intestine in region of oesophageal glands narrow and apparently lacking lumen**. A postvulval uterine sac present. Crustaformeria in form of a quadricolumella with four cells in each of four rows. Ovary and testis outstretched, with one or two rows of cells. Tails elongate-conoid to filiform. Bursa adanal to subterminal. Fungal feeders and associates of insects and plant roots.

**Type species***Safianema lutonense* Siddiqi, 1980syn. *Pseudhalenchus lutonensis* (Siddiqi) Ryss & Krall, 1981*Ditylenchus lutonensis* (Siddiqi) Fortuner, 1982**Other species***Safianema acutum* (Khan & Nanjappa, 1972) Siddiqi, 1986syn. *Pseudhalenchus acutus* Khan & Nanjappa, 1972*Ditylenchus acutus* (Khan & Nanjappa) Fortuner, 1982*Ditylenchus acuminatus* Fortuner & Maggenti, 1987 (= junior objective syn.)*S. anchilisposoma* (Tarjan, 1958) Siddiqi, 1980syn. *Pseudhalenchus anchilisposoma* Tarjan, 1958 (original spelling *anchilisposomus*)*Ditylenchus anchilisposoma* (Tarjan) Fortuner, 1982*S. apus* (Brzeski, 1991) comb. n.syn. *Ditylenchus apus* Brzeski, 1991*S. damnatum* (Massey, 1966) Siddiqi, 1980syn. *Pseudhalenchus damnatus* Massey, 1966*Ditylenchus damnatus* (Massey) Fortuner, 1982*S. indicum* (Sethi & Swarup, 1967) Siddiqi, 1986syn. *Pseudhalenchus indicus* Sethi & Swarup, 1967*Ditylenchus indicus* (Sethi & Swarup) Fortuner, 1982

ETYMOLOGY. Named after my daughter, Miss Safia Fatima Siddiqi, who collected the type species.

*Safianema lutonense* was collected from peaty soil under oak at Luton, England.



**Fig. 50.** *Safianema lutonense* Siddiqi. A and B. Female and male head ends, respectively. C. Spicular region. D. Female oesophagus. E. Female. F. Female anal region. G–I. Female tails. J. Male tail. K. Vulval region. (After Siddiqi (1980a), courtesy Helminthological Society of Washington.)

**Genus *Diptenchus* Khan, Chawla & Seshadri, 1969**

(Fig. 51, A–C)

**Diagnosis**

Anguininae. Body slender, ventrally arcuate on death, about 1 mm long. **Lateral field with five incisures**. Cephalic region low flat, continuous; framework not sclerotized, with six equal sectors. Stylet very weak, 8–9  $\mu\text{m}$  long in type species, **knobs in the form of slight thickenings**. Orifice of dorsal gland about 2  $\mu\text{m}$  from stylet base. Median bulb ovate, muscular, valvate, anterior to middle of oesophagus. Basal bulb pyriform. Isthmus about as long as corpus. Excretory pore near base of oesophagus in type species. Vulva at 82–86% in type species; vagina directed forward. **Postvulval uterine sac absent**. Ovary outstretched or reflexed at tip, oocytes in a row. Vulva–anus distance about one tail length. Tail conical with pointed tip. Bursa enveloping two-thirds of tail in type species. Spicules 22  $\mu\text{m}$ , gubernaculum 8  $\mu\text{m}$  long in type species.

**Type species**

*Diptenchus indicus* Khan, Chawla & Seshadri, 1969

syn. *Ditylenchus khani* Fortuner, 1982 (was a nom. nov.)

No other species.

**Remark**

*Diptenchus* is unique amongst Anguininae in lacking a postvulval uterine sac and having the vagina directed anteriorly.

ETYMOLOGY. *Dipt* from first letters of *Ditylenchus*, *Psilenchus* and *Tylenchus*, to which it was originally thought to be close, and Greek *enchos* = spear.

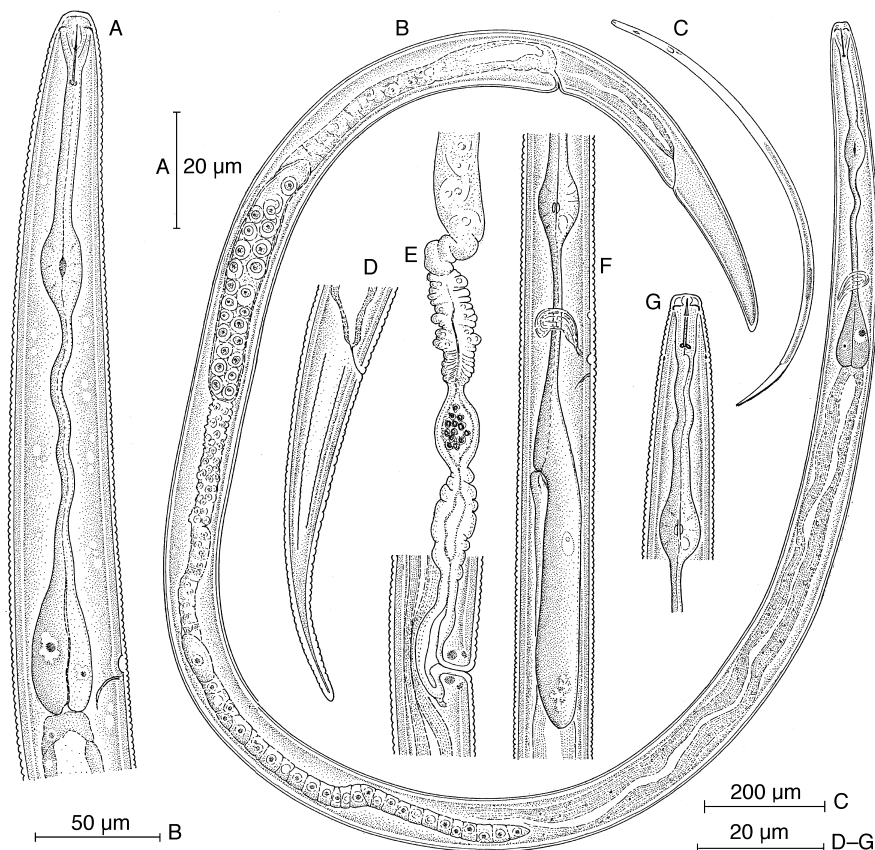
The type species was found around roots of *Vitis vinifera* in New Delhi, India.

**Genus *Pseudhalenchus* Tarjan, 1958**

(Fig. 51, D–G)

**Diagnosis**

Anguininae. Body small (0.3–0.8 mm);  $a < 40$ . Lateral field with four incisures, not areolated. Cephalic region low, rounded, finely striated; framework lightly sclerotized. Amphidial apertures small longitudinal slits on labial plate. Stylet slender, less than 12  $\mu\text{m}$  long; conus without distinct lumen, shorter than shaft, knobs distinct, rounded. Median bulb oval, muscular, valvate. Isthmus slender. **Dorsal oesophageal gland elongated, lying free in body cavity, extending over anterior end of intestine**; subventral glands neither enlarged, nor extending over intestine. Cardia absent. Excretory pore behind nerve ring. Vulva at 72–74% in type species. Postvulval uterine sac present. **Spermatheca rounded but axial**; sperm small or moderately large, rounded. Quadricolumella present. Ovary outstretched. Rectum and anus distinct. Tails in both sexes elongate-conoid. Bursa adanal, may extend to one-third of tail. Spicules slender, arcuate, cephalated. Gubernaculum small, fixed.



**Fig. 51.** A–C. *Diptenchus indicus* Khan, Chawla & Seshadri, paratype female. D–G. *Pseudhalenchus minutus* Tarjan, paratype female. A. Oesophageal region. B. Female. C. Female in death position. D. Tail end. E. Vulval region and genital organs. F. Basal region of oesophagus. G. Head end.

#### Type species

*Pseudhalenchus minutus* Tarjan, 1958

#### Other species

*Pseudhalenchus hylobii* Massey, 1967

syn. *Safianema hylobii* (Massey) Siddiqi, 1980

*P. insolitus* Mukhina & Morokhovets, 1985

*P. leevalleyensis* Grewal, 1991

*P. scrjabini* (Nesterov & Kozhokane, 1980) Siddiqi, 1986

syn. *Radopholoides scrjabini* Nesterov & Kozhokane, 1980

*P. siddiqii* Grewal, 1991

ETYMOLOGY. From Greek *pseudes* = false, and *Halenchus*.

The type species was found in soil and organic debris in a citrus grove, north of Star Lake, Lake-of-the-Hills, Florida, USA. Grewal (1991) gave a key to species of *Pseudhalenchus*.

### Genus *Nothanguina* Whitehead, 1959

(Fig. 52)

#### Diagnosis

Anguininae. Body about 1–2 mm long; female partially obese, stout, ventrally spirally coiled; male less stout, dorsally or irregularly curved when relaxed. Cuticle finely annulated. Cephalic region smooth, flat cap-like, continuous or slightly offset from body. Stylet about 8–10  $\mu\text{m}$  long; conus pointed, knobs rounded. **Corpus non-muscular**, with or without a fusiform non-valvate swelling posteriorly, no median oesophageal bulb. Basal bulb offset from intestine or base slightly extending over intestine dorsally. Excretory pore behind nerve ring. Vulva a long transverse slit, at 88–93% of body length; lips raised, rounded; no lateral membranes. Postvulval uterine sac prominent. Crustaformeria with more than four cells in each of four rows. Female tail conoid. Spicules moderately strong, 28–30  $\mu\text{m}$  long in type species. **Gubernaculum absent. Bursa adanal**, usually extending to middle of tail. Eggs 85–100  $\mu\text{m}$  long, 31–38  $\mu\text{m}$  wide in type species. First- and second-stage juveniles of type species 0.53–0.66 mm and 0.74–0.81 mm long, respectively. Second-stage infective juveniles occur in large numbers in mature galls.

#### Type species

*Nothanguina cecidoplastes* (Goodey, 1934) Whitehead, 1959

syn. *Anguillulina cecidoplastes* Goodey, 1934

*Anguina cecidoplastes* (Goodey) Filipjev, 1936

No other species.

ETYMOLOGY. From prefix of *Nothotylenchus* (which it resembles in lacking a median oesophageal bulb), and *Anguina*.

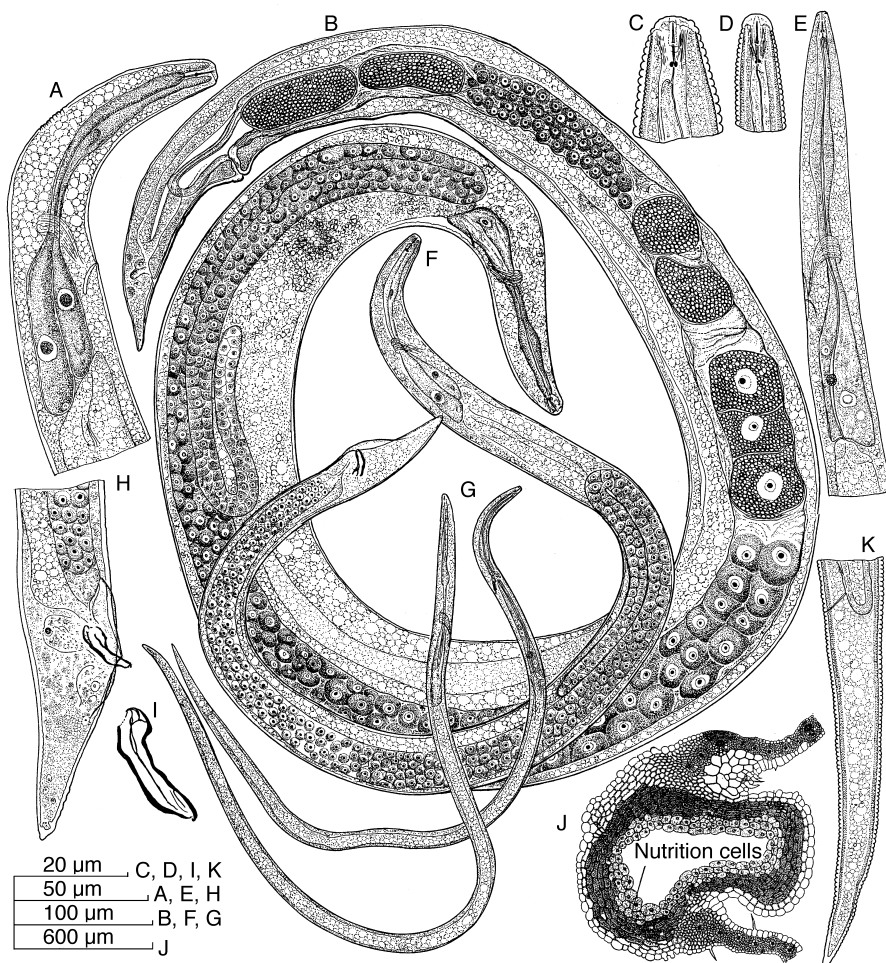
The type species parasitizes *Bothriochloa pertusa* (= *Andropogon pertusus*), a common pasture grass in south India. The galls are produced on leaves, leaf sheaths, stems and on the axis of the inflorescence; on one leaf blade up to 40 galls can be found. Galls are colourless when young but turn purple to purplish black later. Mature galls contain one to five females and as many males and numerous eggs and juveniles; old galls contain only second-stage juveniles and cuticles of dead adults.

### Genus *Orrina* Brzeski, 1981

(Fig. 53, A–E)

#### Diagnosis

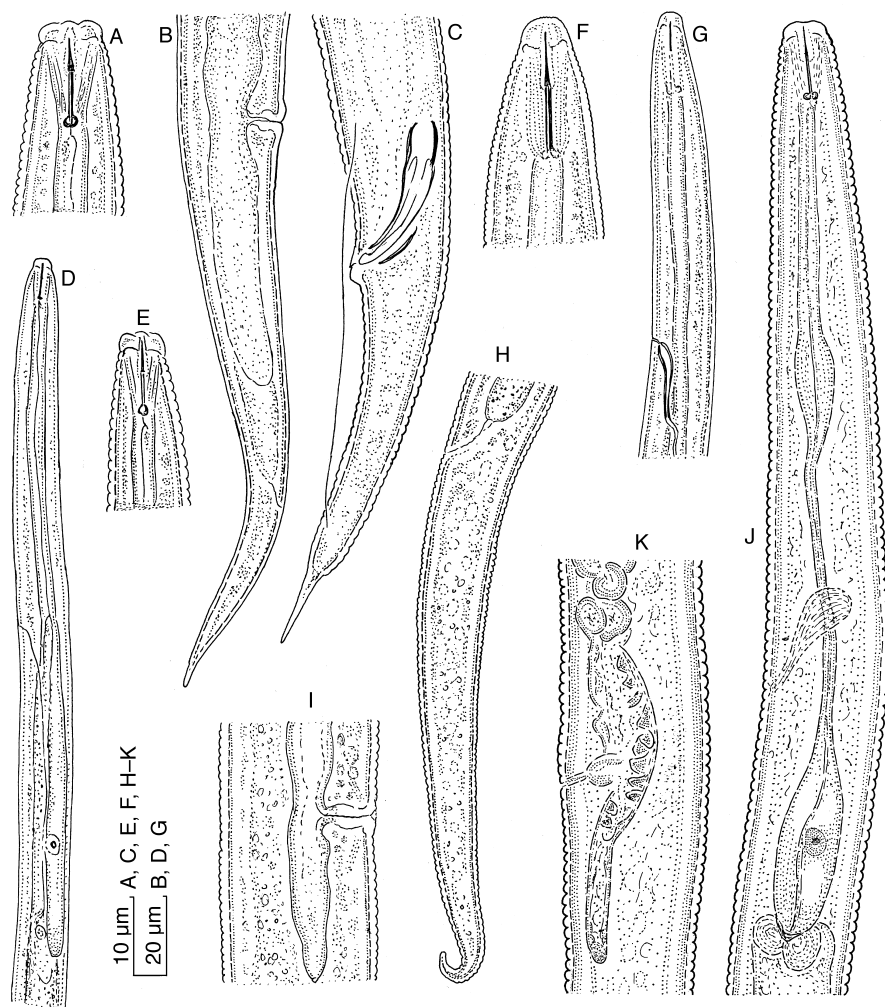
Anguininae. Body about 1 mm or less long, slender ( $a = 20\text{--}30$ ), straight to ventrally arcuate when relaxed. Cuticle finely striated. **Lateral fields narrow, with four**



**Fig. 52.** *Nothanguina cecidoplastes* (Goodey) from leaf-galls of *Bothriochloa pertusa* from India. A. Oesophageal region of male. B. Entire female. C and D. Head ends of male and second-stage juvenile, respectively. E and K. Oesophageal region and tail end of second-stage juvenile, respectively. F. Entire male. G. Second-stage juveniles. H. Tail end of male. I. Spicule. J. Vertical transverse section of a portion of leaf and well-developed gall on *Bothriochloa pertusa* due to *Nothanguina cecidoplastes*. (J. After T. Goodey (1934); remainder after Siddiqi (1986).)

**incisures.** Cephalic region flat, cap-like, slightly offset by narrowing of head contour. Stylet about as long as cephalic region width, distinctly knobbed. **Corpus cylindroid, muscular median bulb absent.** Oesophageal glands extending over intestine; subventrals small. Vulva at about 82% of body length. A well-developed postvulval uterine sac present. Spermatheca elongated, axial. Ovary outstretched, oocytes in one or two rows. Female tail conoid. Male more slender than female.





**Fig. 53.** A–E. *Orrina phyllobia* (Thorne) from galls on *Solanum elaeagnifolium* from Lubbock, Texas, USA. F–I. *Halenchus fucicola* (de Man & Barton in de Man, 1892) from galls on sea weeds from Irish coast. J and K. *Nothotylenchus oryzae* (Mathur, Khan & Prasad), holotype female. A and F. Anterior ends of females. B and H. Tail ends of females. C. Tail end of male. D and E. Oesophageal region and head end of second-stage juvenile respectively. G. Anterior region of female showing sclerotized excretory duct. I and K. Vulval regions. J. Oesophageal region of female.

Bursa subterminal. Spicules cephalated, slightly arcuate. Gubernaculum trough-like. Fourth-stage juveniles are the resistant (dauer) stage. Parasites of plant shoot.

#### Type species

*Orrina phyllobia* (Thorne, 1934) Brzeski, 1981

syn. *Anguillulina phyllobia* Thorne, 1934

*Ditylenchus phyllobius* (Thorne) Filipjev, 1936

*Nothanguina phyllobia* (Thorne) Thorne, 1961

No other species.

### Species inquirenda

*Tylenchus dipsaci* var. *tobaensis* Schneider, 1937

syn. *Ditylenchus dipsaci* var. *tobaensis* (Schneider) Kirjanova, 1951 (parasitizes *Potamogeton mucronatus* and *Myriophyllum spicatum* in Sumatra, Indonesia; probably belongs to *Orrina*)

ETYMOLOGY. Patronym honouring C.C. Orr.

Thorne (1961) estimated 842,000 *O. phyllobia* in a single infested leaf of *Solanum elaeagnifolium* in Arizona and Texas, USA; it also occurs in India on the same host.

### Genus *Pterotylenchus* Siddiqi & Lenné, 1984

(Figs 8(a)C; 49, C; 54)

#### Diagnosis

Anguininae. Under 1 mm, slender (type species female: 0.56–0.8 mm; a = 22–35), straight to slightly arcuate when relaxed. Cuticle and subcuticle finely annulated. Lateral field with four incisures, inner incisures close together. Deirids present. Cephalic region low, smooth, continuous. Stylet small (8–11 µm long in type species) with round basal knobs. Corpus cylindroid, may have a non-muscular, non-valvate slight swelling posteriorly. Basal bulb elongate, saccate; dorsal gland extending over intestine for about one body width in type species. **Large prominent lateral vulval flaps present**, partially covering vulva. Vulva a long transverse slit, posterior (at 80–84% in type species), vagina at right angles to body axis. Postvulval uterine sac prominent. Crustaformeria of four rows of eight to nine cells each. Spermatheca elongate-axial, empty. Ovary outstretched; oocytes in a row. Female and juvenile tails elongate-conoid, pointed, about three to five anal body widths long. Second-stage juveniles similar to female in most details, with shorter dorsal gland and less sharply pointed tail in type species. Male not known. Gall-inciting on aerial parts of plants.

#### Type species

*Pterotylenchus cecidogenus* Siddiqi & Lenné, 1984

No other species.

ETYMOLOGY. From Greek *pteron* = wing (for vulval flaps), and *Tylenchus*.

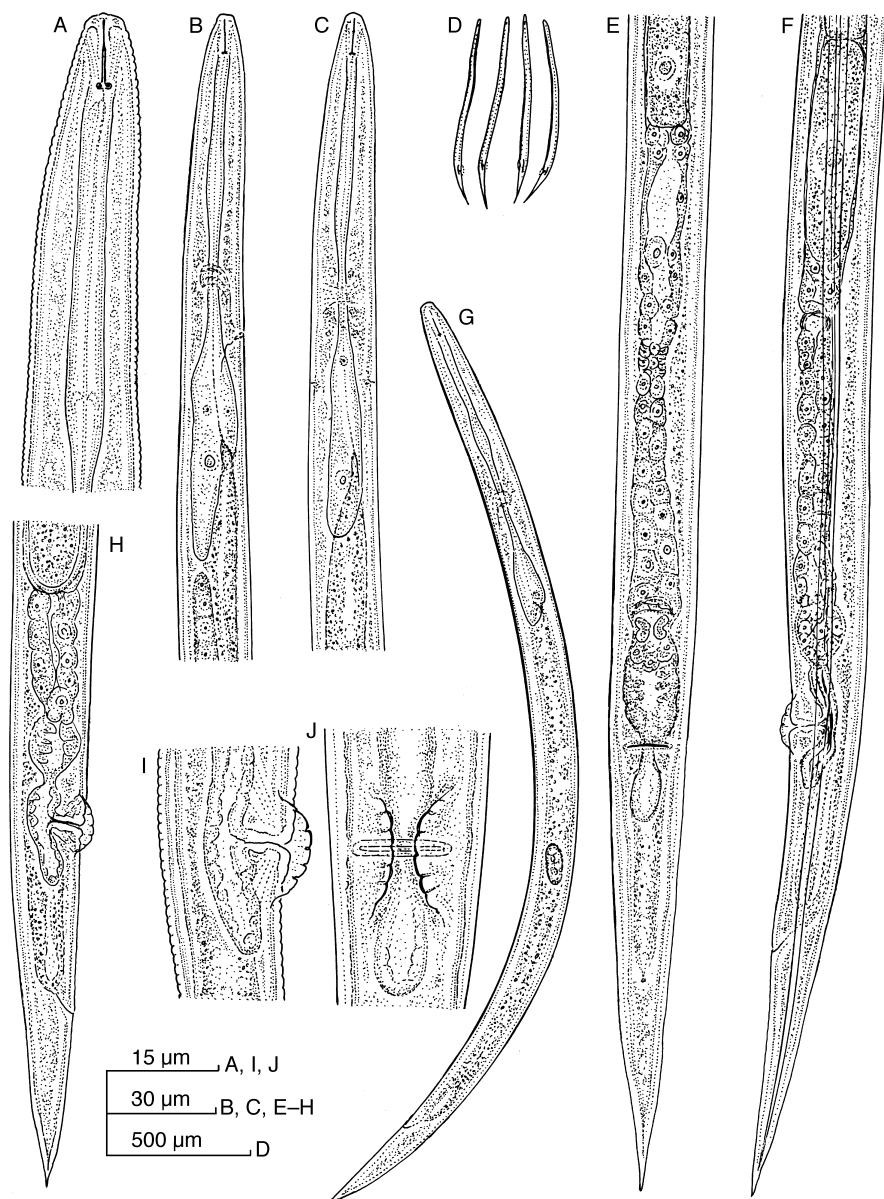
The type species forms galls on the stem of *Desmodium ovalifolium* Wall., a tropical pasture legume, in Llanos Orientales, Colombia. The galls, 0.5–2 cm in diameter, are formed on nodes and stem divisions and contain a large number of females and juveniles in all stages of development.

### Genus *Indoditylenchus* Sinha, Choudhury & Baqri, 1985

(Fig. 48, F–H)

#### Diagnosis

Anguininae. Body under 1 mm long, slender, straight to slightly arcuate when relaxed. Cuticle and subcuticle finely annulated. Lateral field with four incisures.



**Fig. 54.** *Pterotylenchus cecidogenus* Siddiqi & Lenné. A–C. Head ends of females. D. Females. E, F and H. Tail ends of females. G. Second-stage juvenile. I and J. Vulval regions showing lateral vulval flaps. (A–J. After Siddiqi and Lenné (1984), courtesy *Journal of Nematology*.)

Cephalic region low, smooth, continuous. Stylet small (11–12.5 µm long in type species) with round basal knobs. Median oesophageal bulb with refractive thickenings. Basal bulb pyriform to saccate, offset from intestine. **Excretory pore anterior to median oesophageal bulb, 4.5–6.8 head widths from anterior end.** Vagina at

right angles to body axis. Postvulval uterine sac prominent. Spermatheca elongate-axial. Ovary outstretched; oocytes in a row. Female, male and juvenile tails elongate-conoid, pointed, over five anal body widths long. Spicules 18–22  $\mu\text{m}$  long in type species. Gubernaculum small, linear, 6–8  $\mu\text{m}$  long. Bursa adanal, enveloping about two-fifths of tail.

#### Type species

*Indoditylenchus sundarbanensis* Sinha, Choudhury & Baqri, 1985

No other species.

ETYMOLOGY. The generic name is derived from India = country of its origin, and *Ditylenchus*.

The type species was found in a virgin mangrove swamp in Prentice Island, Sundarbans, West Bengal, India. The male of the type species was described from the type locality by Sinha *et al.* (1991).

### SUBFAMILY HELENCHINAE

#### (Marine Anguinidae forming galls on seaweeds)

The subfamily Helenchinae is unique among the Tylenchida in having members that parasitize marine plants. This is the only example of Tylenchida flourishing in a marine habitat and represents a unique derived character in Tylenchida. Other Tylenchida reported from a marine habitat (e.g. *Hirschmanniella marina*) are chance occurrences since they have a large number of related species on the land. The wide sclerotized terminal region of the excretory duct, prehensile tail and the marine habitat justify, contrary to Fortuner & Raski's (1987) contention, a separate subfamily for *Halenchus*.

The genus *Halenchus* has three species which are exclusively marine and which produce galls on seaweeds (algae). *Halenchus fucicola* was found by Barton (1892) in galls of *Ascophyllum nodosum*, a brown alga, on the east and west coast of Scotland. It was described as *Tylenchus fucicola* by de Man in 1892. Two other species closely similar to *H. fucicola* and known from western Europe are *H. dumnonicus* and *H. mediterraneus*.

Coles (1958) found *H. dumnonicus* in galls on *Fucus vesiculosus* on the British southeastern coast. This seaweed occurs in the middle zone of the shore. The rough galls are produced on the thallus, usually on the stipes and less frequently on the base of the fronds. The galls are lighter in colour than the surrounding plant tissues and contain a hollow space in which the nematodes live.

*Halenchus fucicola* can be cultured on *Ascophyllum nodosum* in sea water in the laboratory at 10–16°C; attempts to culture it on fungi or plants such as cabbage, peanut, potato and tomato were unsuccessful (Davide, 1980).

## Subfamily Halenchinae Jairajpuri & Siddiqi, 1969

### Diagnosis

Anguinidae. About 1 mm long, slender, vermiform; no marked sexual dimorphism. Cephalic region smooth; framework hexaradiate, sectors almost equal. Stylet knobbed. No muscular valvate median bulb. Dorsal oesophageal gland large, lobe-like, extending over intestine. **Excretory duct wide, sclerotized, opening through large pore** behind nerve ring. Vulva a long, transverse slit, postmedian at less than 80% of body. Postvulval uterine sac present. Ovary outstretched. **Tail similar between sexes, elongate-conoid, with tip characteristically hooked ventrally.** Bursa not enclosing tail tip. **Exclusively marine, inciting galls on seaweeds.**

### Type genus

*Halenchus* N.A. Cobb in M.V. Cobb, 1933

No other genus.

### Genus *Halenchus* N.A. Cobb in M.V. Cobb, 1933

syn. *Anguillulina* (*Halenchus* Cobb, 1933) (Schneider, 1939)

(Figs 49, D; 53, F–I)

### Diagnosis

Halenchinae. With characters of the family. About 0.5–1.5 mm long, slender, vermiform. Cuticle finely striated; lateral field narrow, with four incisures. Cephalic region continuous or slightly offset, smoothly rounded; framework lightly sclerotized. Stylet well developed, 14–18  $\mu\text{m}$  long in type species, 20–25  $\mu\text{m}$  long in *H. dumonicus*; conus about half stylet length; knobs rounded. Orifice of dorsal gland 2–3  $\mu\text{m}$  behind stylet base. Corpus cylindrical, non-muscular, with a basal non-valvate fusiform swelling. Isthmus slender. **Oesophageal glands free, dorsal gland large, extends over intestine dorsally or subdorsally.** Excretory pore prominent, transversely oval, behind nerve ring; **excretory duct strongly sclerotized** for about one body width and dilated near excretory pore. Vulva at about 60–64% in type species. Postvulval uterine sac about one body width long in type species. Quadricolumella present. Spermatheca elongate, axial. Ovary outstretched, oocytes mostly in single file. Rectum and anus distinct. Tail elongate-conoid, 45–91  $\mu\text{m}$  long in type species; tip finely rounded and hooked ventrally or laterally. Male with single outstretched testis producing moderately large, round sperm. Spicules 19–28  $\mu\text{m}$  long. Gubernaculum simple, 5–7  $\mu\text{m}$  long, fixed. Bursa adanal, extending to about middle of tail. Eggs 75–80  $\times$  23–24  $\mu\text{m}$ . Second-stage juveniles 330–350  $\mu\text{m}$  long, with 11  $\mu\text{m}$  long stylet and hook-like tail tip. Obligate endoparasites of marine algae (seaweeds), inciting and inhabiting galls.

### Type species

*Halenchus fucicola* (de Man & Barton in de Man, 1892) N.A. Cobb in M.V. Cobb, 1933

syn. *Tylenchus fucicola* de Man & Barton in de Man, 1892

*Anguillulina fucicola* (de Man & Barton in de Man) Goodey, 1932

### Other species

*Halenchus dumnonicus* Coles, 1958

*H. mediterraneus* (Micoletzky, 1922) N.A. Cobb in M.V. Cobb, 1933

syn. *Tylenchus mediterraneus* Micoletzky, 1922

*Anguillulina mediterranea* (Micoletzky) Goodey, 1932

### Note

*Halenchus* was transferred to Neotylenchoidea by Sumenkova (1974) because the isthmus was reduced and the oesophageal glands were lying separate from the oesophagus. *Halenchus mexicanus* Chitwood, 1951 has been transferred to the genus *Hirschmanniella* by Sher (1968).

ETYMOLOGY. From Greek *hals* = salt, sea, and *enchos* = spear.

The type species was found by Barton (1892) in galls of *Ascophyllum nodosum*, a brown alga, on the east and west coast of Scotland.

## Genus inquirendum in Anguinidae

### Genus *Chitinotylenchus* Micoletzky, 1922

syn. *Tylenchus* (*Chitinotylenchus* Micoletzky, 1922)

*Anguillulina* (*Chitinotylenchus* Micoletzky) (Schneider, 1939)

*Chitinotylenchus* was proposed by Micoletzky (1922) as a subgenus of *Tylenchus*. Micoletzky (1922) described *T. (Chitinotylenchus) paragracilis* Micoletzky, 1922 and included under the subgenus eight other species of *Tylenchus* (*T. coffeae* Zimmermann, 1898; *T. gracilis* de Man, 1880; *T. mahogani* Cobb, 1920; *T. musicola* Cobb, 1919; *T. penetrans* Cobb, 1917; *T. sacchari* Soltwedel, 1888; *T. similis* Cobb, 1893 and *T. symmetricus* Cobb, 1914). Filipjev (1936) proposed the combination *Chitinotylenchus paragracilis* (Micoletzky, 1922) and designated *C. paragracilis* as the type species of *Chitinotylenchus*. He (1936) also proposed the combination *Chitinotylenchus annulatus* (Cassidy, 1930). Micoletzky characterized the subgenus by the chitinized cephalic framework but Filipjev (1936) distinguished *Chitinotylenchus* on the basis of the bifurcated base of the stylet and this has since been the main distinguishing character of the genus. Golden (1971) used this character in differentiating *Chitinotylenchus* from 19 other genera of the family Tylenchidae.

Sher (1970) re-studied the original specimen (= holotype) of *T. paragracilis*, found it to belong to the genus *Ditylenchus* and proposed the synonymy of *Chitinotylenchus* Micoletzky, 1922 with *Ditylenchus* Filipjev, 1936. Later, Loof & Sher (1971) applied to the International Commission on Zoological Nomenclature for the validation of *Ditylenchus* by the suppression of *Chitinotylenchus* (Bull. Zool. Nom. 28, 112–113). In reply to the letters from the Commission's Secretary, I gave my reasons in favour of rejecting Sher's proposed synonymy of *Chitinotylenchus* with *Ditylenchus* and added that it was difficult to identify *Chitinotylenchus* with *Ditylenchus* since information was lacking on such structures as uterus, spermatheca, sperm, male tail and lateral fields, while Andr ssy argued for regarding *Chitinotylenchus paragracilis* Micoletzky, 1922 as *genus et species inquirendae*. The

Commission finally ruled that *Ditylenchus* should be given nomenclatural precedence over *Chitinotylenchus* whenever the two names are considered synonyms and that *Chitinotylenchus* should be placed on the Official List of Generic Names in Zoology with an endorsement that it is not to be given priority over *Ditylenchus* whenever the two names are regarded as synonyms (Opinion no. 1184, *vide* Melville, 1981).

#### Type species

(subsequent designation by Filipjev, 1936)

- Chitinotylenchus paragracilis* (Micoletzky, 1922) Filipjev, 1936
- syn. *Tylenchus* (*Chitinotylenchus*) *paragracilis* Micoletzky, 1922
- Anguillulina paragracilis* (Micoletzky) Goodey, 1932
- Ditylenchus paragracilis* (Micoletzky) Sher, 1970

#### Present status

Species inquirenda.

#### Species inquirendae

- Chitinotylenchus boevii* Izatullaeva, 1967
- syn. *Ditylenchus boevii* (Izatullaeva) Tarjan & Hopper, 1974 (wrongly attributed to Sher, 1970)
- C. clavatus* Nesterov, 1979
- C. incognatus* (van der Linde, 1938) Loof, 1956
- syn. *Anguillulina incognata* van der Linde, 1938
- Ditylenchus incognatus* (van der Linde) Hopper & Tarjan, 1974 (wrongly attributed to Sher, 1970)
- C. sedatus* Kirjanova, 1951
- syn. *Ditylenchus sedatus* (Kirjanova) Tarjan & Hopper, 1974 (wrongly attributed to Sher, 1970)

#### Nomina nuda

- Chitinotylenchoides* Arias & Jiménez-Millán, 1968 (= *Tylopharynx* (Diplogasterida))
- Chitinotylenchoides mediterraneensis* Arias & Jiménez-Millán, 1968

## FAMILY SYCHNOTYLENCHIDAE

**(Anguinoidea with prominent median oesophageal bulb, spicule as long as tail, found associated with bark beetles)**

The family comprises *Ditylenchus*-like forms which are found in frass of bark beetles. They are fungal feeders and have a direct life cycle as do other Anguinoidea. The median bulb is very muscular and often large, bearing large refractive thickenings. They have short tails in adults but elongate to filiform tails in juveniles. The female tail is generally cylindroid or subcylindroid, while that of the male is tapering and completely enveloped by a bursa, a character which immediately distinguishes this group from the other Anguinoidea. The male tail may be shorter than the spicule.

These nematodes have a slow rate of development, produce no more than three

to four generations per year and are generally found in low numbers. According to Rühm (1956), third-stage juveniles occur as dauerlarvae under the elytra and between the terga of bark beetles, the beetles acting as carriers for the nematodes.

Members of this family are not found in insect-free environments. Their association with xylophagous and mycetophagous insects perhaps is not just commensalism but is much more intricate. These nematodes are very similar to the members of the Paurodontidae and the free-living forms of the Sphaerularioidea (cf. *Prothallonema*) and could be suspected of having an insect-parasitic generation. The genus *Neomisticus* Siddiqi, 1986 of the Paurodontidae is very similar to *Sychnotylenchus*, differing in the absence of a muscular median bulb. Similarly, *Luella* and *Paurodontoides* of the Paurodontidae have affinities with the members of the Sychnotylenchidae. However, since an insect-parasitic generation has not yet been observed in the Sychnotylenchidae and the muscular median bulb-bearing forms are not known in the Hexatylna, I consider this family as ecologically intermediate between Anguinoidea and Sphaerularioidea.

## Family Sychnotylenchidae Paramonov, 1967 syn. Neoditylenchidae Kakuliya & Devdariani, 1975

### Diagnosis

Anguinoidea. Adults 0.5–2.5 mm long, slender. Cuticle finely annulated, annules may be distinct. Cephalic region low, smooth; framework hexaradiate, often moderately sclerotized, lateral sectors may be offset from precorpus by a constriction. Isthmus usually short. Basal bulb generally large, saccate, offset from intestine, lacking a stem-like extension at base. **Vulva at 88–94% of body length**, lacking lateral cuticular flaps. Postvulval uterine sac present. Quadricolumella with six or more cells in each row. Ovary outstretched or reflexed, oocytes not arranged about a rachis. **Female tail small, cylindroid or subcylindroid**, occasionally conoid but with rounded tip. **Male tail conoid, completely enveloped by a bursa**. Juveniles with generally elongate-conoid tails; third- or fourth-stage as dauerlarvae. Associates of insects (mostly bark beetles).

### Type subfamily

Sychnotylenchinae Paramonov, 1967

No other subfamily.

### Note

The subfamily Sychnotylenchinae was raised to the family rank by Golden (1971) and Siddiqi (1971). Sychnotylenchidae was also proposed by Kakuliya & Devdariani, 1975.



## Subfamily Sychnotylenchinae Paramonov, 1967 syn. Neoditylenchinae Kakuliya & Devdariani, 1975

### Diagnosis

Sychnotylenchidae, with characters of the family.

### Type genus

*Sychnotylenchus* Rühm, 1956

### Other genus

*Neoditylenchus* Meyl, 1961

### Key to genera of Sychnotylenchinae

1. Lateral sectors of cephalic framework conspicuously narrower than sub-medians; excretory pore opposite median oesophageal bulb or more anterior ..... *Sychnotylenchus*  
Lateral sectors of cephalic framework not narrower than submedians; excretory pore behind median oesophageal bulb ..... *Neoditylenchus*

### Genus *Sychnotylenchus* Rühm, 1956

syn. *Sychnotylenchus* Rühm, 1955 (= nomen nudum)

(Fig. 55)

### Diagnosis

Sychnotylenchinae. Medium-sized (0.7–1.2 mm). Cephalic region low, offset; framework sclerotized; **lateral sectors characteristically narrower than the submedians**; lateral lip areas slightly raised. Stylet with strongly developed shaft, conus symmetrical with solid appearance, knobs generally small, elongated, rarely indistinct. Precorpus gradually widening from stylet base to near postcorpus or median bulb. Median bulb muscular, with crescentic refractive thickenings. Basal bulb large, offset from intestine. **Excretory pore opposite median bulb or more anterior**. Renette cell just posterior to nerve ring. Vulva far posterior at 89–94% of body length, lips prominent. Postvulval uterine sac well developed. Quadricolumella with eight or more cells in each row. Female tail short, broadly rounded. Male tail short, conoid, completely enveloped by a large bursa. Spicules cephalated, slender in distal two-thirds, **about as long as tail**. Associates of bark beetles.

### Type species

*Sychnotylenchus intricati* Rühm, 1956

syn. *Sychnotylenchus intricati* Rühm, 1955 (= nomen nudum)

### Other species

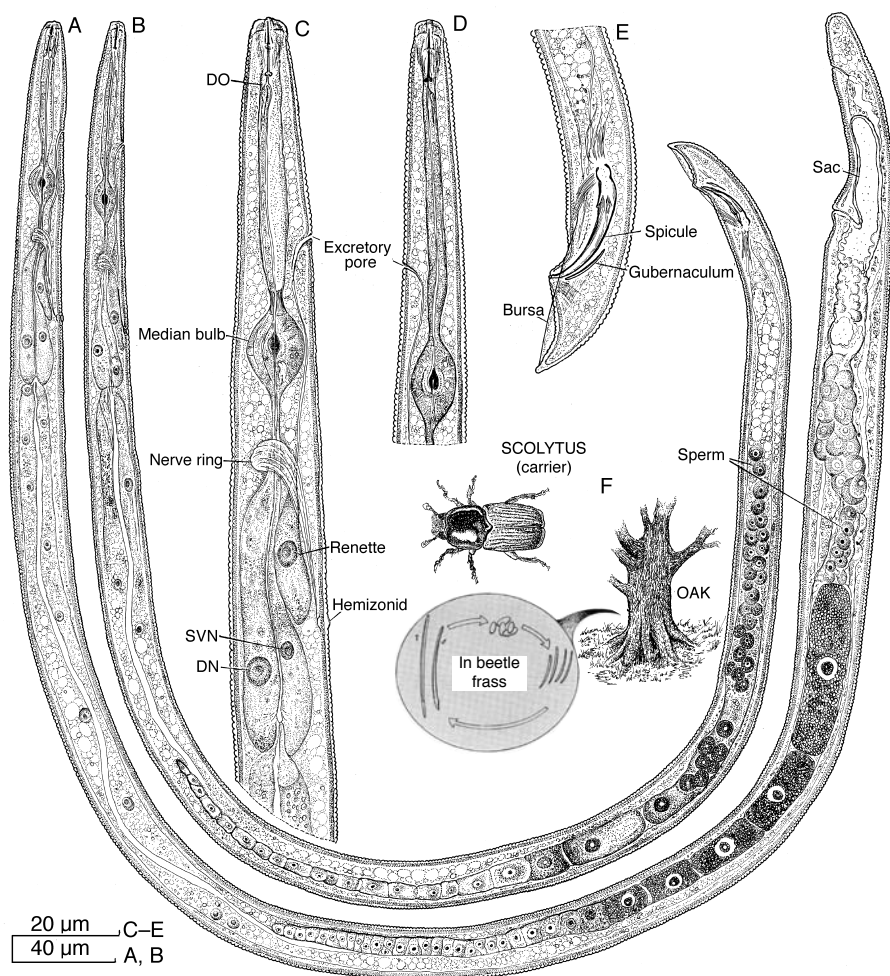
*Sychnotylenchus abietis* Rühm, 1956

syn. *S. abietis* Rühm, 1955 (= nomen nudum)

*S. mutici* Massey, 1974

*S. phloeosini* Massey, 1969

*S. scolyti* Massey, 1969



**Fig. 55.** *Sychnotylenchus intricati* Rühm, from frass of *Scolytus intricatus* on oak in Worcestershire, England. A. Female. B. Male. C. Oesophagus of female. D. Anterior ends of male. E. Posterior end of male. F. Life-history.

*S. ulmi* Rühm, 1956

syn. *S. ulmi* Rühm, 1955 (= nomen nudum)

**ETYMOLOGY.** From Greek *synchos* = plentiful, and *Tylenchus*.

*Sychnotylenchus intricati* was found in large numbers in beetle frass of *Scolytus intricatus* in Germany. Dauerlarvae of *Sychnotylenchus intricati* and *S. ulmi* were found under the elytra and between the terga of the beetle. *Sychnotylenchus abietis* shows commensalism with *Cryphalus abietis*. In the USA, *Sychnotylenchus scolyti* and *S. mutici* lived in beetle galleries of *Scolytus* in American elm and *Gleditsia*, respectively, while *S. phloeosini* was associated with *Phloeosinus* sp. in *Juniperus scopulorum*.

**Genus *Neoditylenchus* Meyl, 1961**

(Fig. 56)

**Diagnosis**

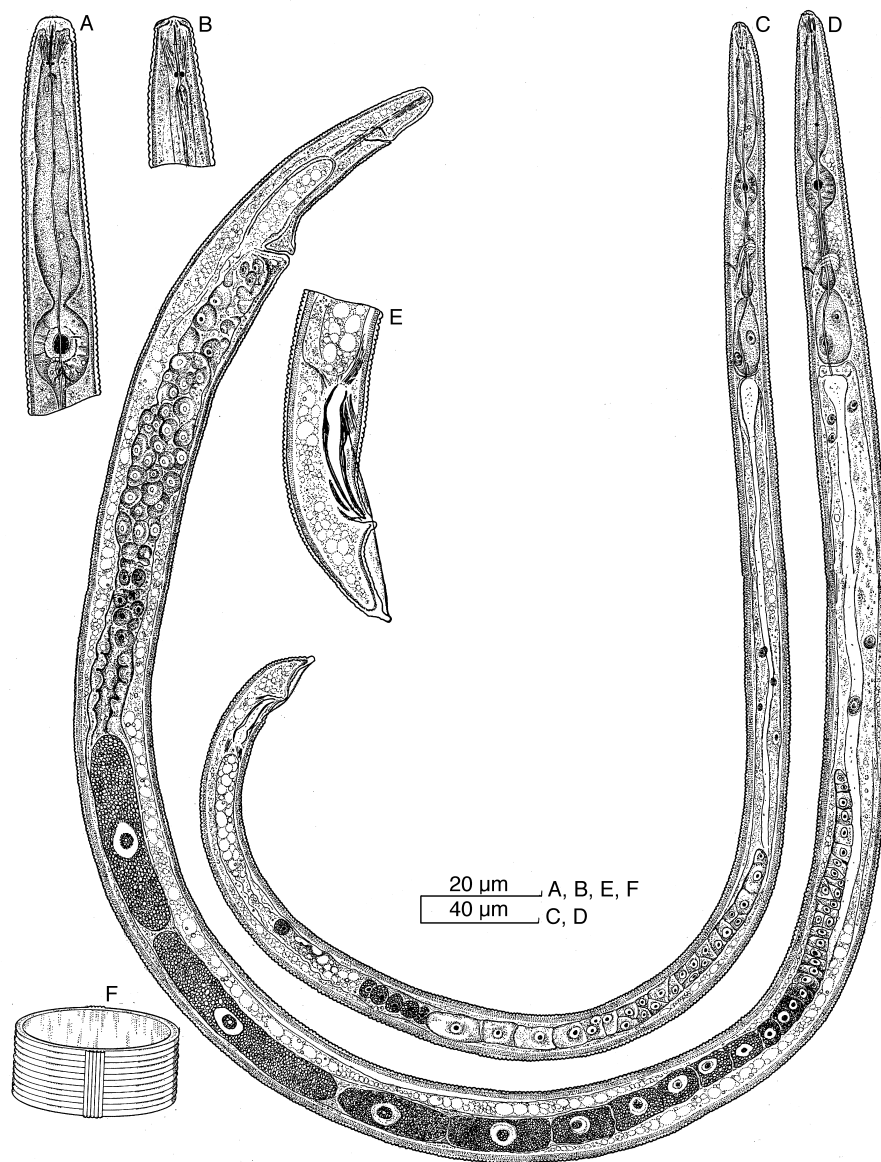
Sychnotylenchinae. Medium to large ( $L = 1\text{--}2.5$  mm), slender. Cuticle smooth or finely striated. Lateral field usually with six incisures, may appear as a plain band or be obscure. Cephalic region smooth or striated, generally continuous with body; **framework** hexaradiate, **with six equal sectors**, light to moderately sclerotized. Stylet small ( $7\text{--}12\text{ }\mu\text{m}$ ), slender, with basal knobs. Orifice of dorsal oesophageal gland a quarter to a half stylet length behind stylet base. Median bulb well developed, muscular, valvate, fusiform or oval. Isthmus elongate-slender. Basal bulb sac-like, often large, offset from intestine, lacking a cardia. **Excretory pore behind nerve ring**. **Vulva** a large transverse slit, **at 89–94% of body length**. Postvulval uterine sac large. Ovary anteriorly outstretched; oocytes in one or several rows, not arranged about a rachis. Vulva–anus distance generally less than two tail lengths. Quadricolumella with six or more cells in each row. Female tail short, cylindroid, subcylindroid or tapering; terminus rounded. Male tail completely enveloped by a bursa. **Spicules about one tail length or longer**. Gubernaculum rod-like or trough-shaped, fixed. Juvenile tails elongate-conoid or filiform.

**Type species**

- Neoditylenchus dendrophilus* (Marcinowski, 1909) Meyl, 1961  
 syn. *Ditylenchus dendrophilus* Marcinowski, 1909  
*Anguillulina dendrophila* (Marcinowski) Goodey, 1932  
*Pratylenchus dendrophilus* (Marcinowski) Filipjev, 1936  
*Ditylenchus dendrophilus* (Marcinowski) Filipjev & Schuurmans Stekhoven, 1941  
*Sychnotylenchus dendrophilus* (Marcinowski) Fortuner & Maggenti, 1987

**Other species**

- Neoditylenchus abieticola* (Rühm, 1956) Meyl, 1961  
 syn. *Ditylenchus abieticola* Rühm, 1956  
*Sychnotylenchus abieticola* (Rühm) Fortuner & Maggenti, 1987  
*N. autographi* (Rühm, 1956) Meyl, 1961  
 syn. *Ditylenchus autographi* Rühm, 1956  
*Sychnotylenchus autographi* (Rühm) Fortuner & Maggenti, 1987  
*N. bimucronatus* Gagarin, 1999  
*N. corniculatus* Massey, 1974  
 syn. *Sychnotylenchus corniculatus* (Massey) Fortuner & Maggenti, 1987  
*N. dalei* Kakuliya & Devdariani, 1975  
*N. dendroctoni* Massey, 1974  
 syn. *Sychnotylenchus dendroctoni* (Massey) Fortuner & Maggenti, 1987  
*N. eremus* (Rühm, 1956) Meyl, 1961  
 syn. *Ditylenchus eremus* Rühm, 1956  
*Sychnotylenchus eremus* (Rühm) Fortuner & Maggenti, 1987  
*N. gallicus* (Steiner, 1935) Meyl, 1961  
 syn. *Anguillulina gallica* Steiner, 1935



**Fig. 56.** *Neoditylenchus petithi* (Fuchs), from frass of *Scolytus mali* in Gloucestershire, England. A. Anterior end of male. B. Head end of female. C. Male. D. Female. E. Tail end of male. F. Lateral field at midbody.

*Ditylenchus gallicus* (Steiner) Filipjev, 1936

*Sychnotylenchus gallicus* (Steiner) Fortuner & Maggenti, 1987

*N. glandarius* Massey, 1974

syn. *Sychnotylenchus glandarius* (Massey) Fortuner & Maggenti, 1987

*N. glischrus* (Rühm, 1956) Meyl, 1961

- syn. *Ditylenchus glischrus* Rühm, 1956  
*Sychnotylenchus glischrus* (Rühm) Fortuner & Maggenti, 1987
- N. major* (Fuchs, 1915) Meyl, 1961  
 syn. *Tylenchus major* Fuchs, 1915  
*Anguillulina major* (Fuchs) Thorne, 1935  
*Ditylenchus major* (Fuchs) Filipjev, 1936  
*Sychnotylenchus major* (Fuchs) Fortuner & Maggenti, 1987
- N. ortus* (Fuchs, 1938) Meyl, 1961  
 syn. *Anguillulina orta* Fuchs, 1938  
*Ditylenchus ortus* (Fuchs) Filipjev & Schuurmans Stekhoven, 1941  
*Sychnotylenchus ortus* (Fuchs) Fortuner & Maggenti, 1987
- N. ovarius* Massey, 1974  
 syn. *Sychnotylenchus ovarius* (Massey) Fortuner & Maggenti, 1987
- N. panurgus* (Rühm, 1956) Meyl, 1961  
 syn. *Ditylenchus panurgus* Rühm, 1956  
*Sychnotylenchus panurgus* (Rühm) Fortuner & Maggenti, 1987
- N. petithi* (Fuchs, 1938) Meyl, 1961  
 syn. *Anguillonema petithi* Fuchs, 1938  
*Ditylenchus petithi* (Fuchs) Rühm, 1956  
*Sychnotylenchus petithi* (Fuchs) Fortuner & Maggenti, 1987
- N. pinophilus* (Thorne, 1935) Goodey, 1963  
 syn. *Anguillulina pinophila* Thorne, 1935  
*Ditylenchus pinophilus* (Thorne) Filipjev, 1936  
*Sychnotylenchus pinophilus* (Thorne) Fortuner & Maggenti, 1987
- N. pityokteinophilus* (Rühm, 1956) Meyl, 1961  
 syn. *Ditylenchus pityokteinophilus* Rühm, 1956  
*Sychnotylenchus pityokteinophilus* (Rühm) Fortuner & Maggenti, 1987
- N. puniwopus* Massey, 1969  
 syn. *Sychnotylenchus puniwopus* (Massey) Fortuner & Maggenti, 1987
- N. rarus* (Meyl, 1954) Goodey, 1963  
 syn. *Ditylenchus rarus* Meyl, 1954  
*Sychnotylenchus rarus* (Meyl) Fortuner & Maggenti, 1987
- N. striatus* (Fuchs, 1938) Meyl, 1961  
 syn. *Anguillonema striatum* Fuchs, 1938  
*Sychnotylenchus striatus* (Fuchs) Fortuner & Maggenti, 1987  
*Ditylenchus striatus* (Fuchs) Rühm, 1954
- N. xylebori* (Roux, 1906) Goodey, 1963  
 syn. *Tylenchus xylebori* Roux, 1906  
*Anguillonema xylebori* (Roux) Rühm, 1955  
*Sychnotylenchus xylebori* (Roux) Ebsary, 1991
- N. yasinskii* Massey, 1969  
 syn. *Sychnotylenchus yasinskii* (Massey) Fortuner & Maggenti, 1987

ETYMOLOGY. From Greek *neos* = young, new, and *Ditylenchus*.

*Neoditylenchus* spp. are found in beetle galleries in tree trunk and their biology is similar to the species of *Sychnotylenchus*.

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# VI Suborder Hoplolaimina

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## SUBORDER HOPLOLAIMINA CHIZHOV & BEREZINA, 1988 syn. *Heteroderata* Skarbilovich, 1959

### Diagnosis

Order Tylenchida. Small to large nematodes (about 0.5–2 mm). Sexual dimorphism in cephalic region present or absent. **Cuticle with distinct outer and inner layers**, often strongly annulated, annules never retrorse. Lateral fields with one to six incisures reducing towards extremities, occasionally reduced or absent (*Basirolaimus*). Cephalic framework well developed, **usually with high arches** and strongly sclerotized and refractive. Labial disc distinct in several genera; with six labial sensilla in the form of papillae or pits present (usually not on surface in Hoplolaimidae) around a pore-like round or oval oral opening; cephalic sensilla usually not on surface. Amphidial apertures pore- or slit-like, just below labial disc, rarely postlabial (*Psilenchus*, *Macrotrophurus*). Deirids generally absent, or present (*Psilenchidae*, *Merliniinae*). **Phasmids present** (not detectable in *Aphasmatylenchus*) **in or near tail region** (except for migratory scutella of some Hoplolaimidae), small, with pore-like apertures, or large, scutellum-like, always in lateral position. **Prophasmids (papilla-like sensilla near vulva) absent**. **Stylet usually well developed; protractors tubular around stylet; basal knobs prominent** (absent in *Psilenchidae*). Orifice of dorsal oesophageal gland close to or at some distance from stylet base. Oesophageal glands free in body cavity or enclosed in a basal bulb. **Postcorporate or median bulb well developed**, muscular, with refractive inner thickenings (except in some males with degenerate oesophagus in Hoplolaimoidea). Intestinal cell walls and lumen usually indistinct; rectum and anus distinct. **Female reproductive system basically didelphic, amphidelphic**; posterior branch may be reduced. Vulva a transverse slit, lips usually not modified, median or submedian, in swollen females may be located subterminally or terminally; epiptygma present or absent. Glandular part of uterus tri- or rarely quadricolumellate. Spermatheca generally axial. Ovaries outstretched in opposite direction, reflexed or coiled in obese

forms. Tails dissimilar between sexes (except Psilenchidae and some Pratylenchidae). Female tail generally short (less than two anal body widths) but may vary to become elongate-conoid or absent in some swollen females. Hypoptygma double. Bursa usually enveloping tail, subterminal, adanal (Psilenchidae) or rarely absent; with or without phasmidial pseudoribs. Testis single (may be double in some *Meloidogyne*), anteriorly outstretched. Spicules paired, similar or rarely dissimilar, cephalated, straight to arcuate, with or without distal flanges, independently protrusible. Gubernaculum simple trough-shaped or modified rod-like, fixed or protrusible, with or without terminal titillae; telamon (= capitulum) present in several genera. **Obligate parasites of plant roots.** No mycetophagy or insect parasitism.

#### Type genus

*Hoplolaimus* von Daday, 1905

#### Type superfamily

Hoplolaimoidea Filipjev, 1934 (Paramonov, 1967)

#### Other superfamily

Dolichodoroidea Chitwood in Chitwood & Chitwood, 1950

#### Relationship

Hoplolaimina differs from Tylenchina, Criconematina and Hexatyline in being didelphic and having phasmids on or near the tail. It also differs from Tylenchina and Hexatyline in being advanced parasites of plant roots. A high-arched, often sclerotized cephalic region, dorsoventrally oval amphidial apertures, cuticle appearing two-layered, usually strong stylet, usual occurrence of axial spermatheca and a tricolomellate glandular part of the uterus also characterize the Hoplolaimina. It can be differentiated from Criconematina by the structure of the oesophagus in females and juveniles, generally well developed male oesophagus, different face-view structures, especially due to the absence of lateral oral liplets and submedian lobes, basic didelphy with spermathecae well formed and not ventrally or subventrally located to gonadial axis, a continuous spermatogenesis in the male, differently shaped spicules, paired hypoptygma on the posterior cloacal lip, and the absence of retrorse annules, cuticular scales, spines or other configurations and of a body sheath and anchor-shaped stylet knobs.

Ecologically Hoplolaimina are recognized as advanced parasites of plant roots. Members of the families Rotylenchulidae, Meloidogynidae and Heteroderidae have developed close physiological relationships with root tissues, females becoming sedentary and obese and male undergoing various morphological adaptations. There is evidence of host specificity and co-evolution with host plants.

#### Key to superfamilies of Hoplolaimina

1. Subventral oesophageal glands enlarged, usually extending past the dorsal gland; sexual dimorphism in anterior region manifest ..... **Hoplolaimoidea**  
Subventral oesophageal glands not enlarged, not extending past the dorsal gland; sexual dimorphism in anterior region not manifest ..... **Dolichodoroidea**

**SUPERFAMILY HOPLOLAIMOIDEA FILIPJEV, 1934 (PARAMONOV, 1967)**  
**syn. Heteroderioidea Filipjev & Schuurmans Stekhoven,**  
**1941 (Golden, 1971)**  
**Hoplolaimoidi (= sub-superfamily proposed by Paramonov,**  
**1967 as Hoplolaimini)**

**Diagnosis**

Hoplolaimina. Small to large nematodes (about 0.5–2 mm). **Sexual dimorphism in cephalic region present**, and in stylet, oesophagus and body shape may also be present, indistinct in some *Pratylenchidae*. **Cuticle with distinct outer and inner layers**, strongly annulated; longitudinal striae may be present but longitudinal ridges outside lateral fields absent. Cephalic framework strongly sclerotized and refractive, generally less developed in males. Labial disc generally offset, distinct; six labial sensilla usually not on the surface. **Cephalic sensilla not on surface. First cephalic annule generally divided into six sectors which may be modified.** Deirids absent (except *Pratylenchoides*). Phasmids small, with pore-like apertures, or large, scutellum-like, always in lateral position, in or near anal region, near tail terminus or much anterior to anus at different levels; absent in *Aphasmatylenchus*. Stylet well developed, two to five times maximum width of lip region; protractors tubular around stylet; conus about as long as shaft, knobs prominent. **Oesophageal glands lobed, overlapping intestine** (except *Pararotylenchus* and some *Pratylenchoides* spp. in which they form a pseudobulb). **Subventral glands enlarged, equal to or usually larger than dorsal gland; nuclei of one or both subventral glands lying posterior to that of the dorsal gland.** Postcorporal or median bulb always well developed (except in some males with degenerate oesophagus), muscular, with refractive thickenings. **A cellular cardia absent**, but oesophago-intestinal junction provided with a small cuticular valvula. Intestine cell walls and lumen usually indistinct; rectum and anus distinct. Female reproductive system basically didelphic, amphidelphic; posterior branch may be reduced or represented by a uterine sac. Vulva a transverse slit, in swollen females may be located subterminally or terminally; epiptygma present or absent; lateral membranes, if present, not conspicuous. **Glandular part of uterus tricolumellate. Spermathecae thick-walled, round, usually axial**, packed spermatozoa often showing cytoplasmic ‘tails’ pointing towards ovary. Ovaries paired, outstretched, reflexed or coiled in obese forms; posterior ovary may be rudimentary. Tails dissimilar between sexes (except some *Pratylenchidae*). Female tail generally short (less than two anal body widths) but may vary to become elongate-conoid, absent in some swollen females. **Male tail usually short and with a distinct hyaline terminal portion.** Bursa enclosing all or most of tail, absent in forms with tail less than one anal body width long (*Meloidogynidae* and *Heteroderidae*). Spicules paired, similar or dissimilar, cephalated, straight to arcuate, with or without distal flanges, independently protrusible. Gubernaculum fixed or protrusible, with or without terminal titillae; telamon (= capitulum) present in several genera.

**Type family**

*Hoplolaimidae* Filipjev, 1934



## Other families

Heteroderidae Filipjev &amp; Schuurmans Stekhoven, 1941

Meloidogynidae Skarbilovich, 1959

Pratylenchidae Thorne, 1949

Rotylenchulidae Husain &amp; Khan, 1967

**Key to families of Hoplolaimoidea**

1. Mature female round, pear- or lemon-shaped behind neck, with anus terminal or nearly so; male with stylet larger than that of female and tail very short or absent, non-bursate (except *Bursadera*). Male develops by metamorphosis (except *Meloidodera*); third- and fourth-stage juveniles often swollen ..... 2  
 Mature female not round, pear- or lemon-shaped, with anus not terminal; male with stylet equal to or smaller than that of female and tail bursate, not very short (except *Verutus*), does not develop by metamorphosis; third- and fourth-stage juveniles normally not swollen ..... 3
2. Excretory pore in mature female opposite or anterior to median bulb; female labial disc dorsoventrally elongated; male with large lip cap and large transverse slit-like amphidial apertures; gall-inciting ..... **Meloidogynidae**  
 Excretory pore in mature female behind median bulb; female labial disc rounded; male with small lip cap and with small oval to round amphidial apertures; not gall-inciting ..... **Heteroderidae**
3. Juveniles and females with low arched cephalic framework, generally endoparasites of roots ..... **Pratylenchidae**  
 Juveniles and females with high arched cephalic framework, generally ectoparasites of roots ..... 4
4. Mature female swollen, sedentary ..... **Rotylenchulidae**  
 Mature female not swollen, migratory ..... **Hoplolaimidae**

## **FAMILY HOPLOLAIMIDAE**

### **(Migratory ectoparasitic Hoplolaimoidea)**

This is a large family of economically important Tylenchida. It comprises three sub-families – Hoplolaiminae, Aphasmatylenchinae and Rotylenchoidinae, which have slender females which are migratory ectoparasites of roots, but some have a tendency to bury themselves in roots. Unlike Pratylenchidae, they are seldom able to move freely within the root tissues and have failed to colonize them, their juveniles and adults occurring in soil. In their ecology and ethology, they are similar to the members of the Dolichodoridae, but the sexual dimorphism in their anterior region and enlarged subventral oesophageal glands, which often extend past the dorsal gland, differentiate them. The enlarged subventral oesophageal glands enable them to penetrate deeper into root tissues and establish a physiological relationship with them.

The Hoplolaimidae penetrate root tissue intracellularly, and reach the inner layers of the cortical tissue by thrusting of the stylet and then the anterior end of the body,

but they do not establish a permanent feeding site by inciting giant cells or syncytia. Their feeding produces single cell damage often with necrotic and brownish lesions. Basically they are ectoparasites which often become spirally curved when relaxed or dead. *Helicotylenchus* spp. feed from a single root hair cell for 40 min. or up to 19 days on deep cortical cells with alternating salivation and ingestion and thus show an evolutionary tendency towards sedentary root parasitism. *Helicotylenchus multicinctus* is able to form cavities in root cortex, where nematodes of all stages and eggs are found.

Newly hatched second-stage juveniles of *Scutellonema cavenessi* invade roots of the host (sorghum, tomato), become endoparasitic and return to the soil as third- or fourth-stage juveniles. They develop to adults in soil and feed on roots as ectoparasites (Demeure *et al.*, 1980). This early-stage endoparasitism appears to be a protective device for the safe development of the early stages.

*Hoplolaimus* spp., the lance nematodes, are found mostly in North and South America. *Hoplolaimus galeatus* parasitizes several field crops (cotton, lucerne, maize), grasses and trees in the USA, where it is of wide occurrence. Cotton plants with a high nematode population show severe stunting, yellowing and defoliation symptoms. The nematodes are found inside the roots as well as in the soil and feed on the cortical and vascular tissues. The nematodes feed ectoparasitically on roots of sycamore and other plants; pine seedlings are killed by high populations. *Hoplolaimus californicus* attacks oak in several localities in California, USA. *Hoplolaimus pararobustus* is widely distributed in Africa (Cameroon, Congo, Kenya, Malawi, Nigeria, South Africa, Tanzania and Zimbabwe). Apparently it is a species-complex representing a polytypic species which, being morphologically different from *Hoplolaimus* and *Basirolaimus* spp., represents a new subgenus *Ethiolaimus*.

*Hoplolaimus* (*Basirolaimus*) spp. are mostly found in South and Southeast Asia and East Africa. One species, *H. (B.) columbus* (the Columbian lance nematode) is common in several states of the USA and also occurs throughout the Indian sub-continent. It is an important parasite of cotton, soybean and sugarcane and attacks a large number of grasses. It feeds both ecto- and endoparasitically on roots and causes extensive damage to root tissues by penetration, migration and feeding. On cotton it feeds ectoparasitically, but on soybean roots it is mostly endoparasitic, penetrating endodermis, pericycle and phloem. In lucerne roots, the nematode feeds ectoparasitically on cortical cells in the maturation zone, and penetrates only a few layers of cells, embedding itself up to the level of the median bulb (Fassuliotis, 1974). It is an important parasite of banana, cabbage, citrus, ragi (*Eleusine coracana*), rice and sugarcane throughout India. It lacks cellulolytic enzymes but can penetrate roots of sugarcane up to the inner layers of the cortex.

*Hoplolaimus (B.) indicus* is more widespread in India than *H. (B.) columbus*. It is a bisexual species that completes its life cycle on sorghum roots in 27–36 days at 28–32°C, whereas *H. (B.) columbus* reproduces parthenogenetically and completes its life cycle on soybean in 45–49 days.

The species of the genus *Rotylenchus* are widespread in colder regions of Western Europe, where *Hoplolaimus* and *Basirolaimus* are uncommon. *Rotylenchus robustus* is an ectoparasite causing damage to carrots, lettuce, lilies, peas, etc. The damage is aggravated in the presence of *Fusarium oxysporum* and other pathogenic fungi. This species prefers a temperature of 13 to 24°C (feeding range 0.5–42.5°C)

and, when present in numbers exceeding  $500 \text{ kg}^{-1}$  soil, is damaging to host plants. At  $27^{\circ}\text{C}$ , feeding involves 245 contractions of the muscular median oesophageal bulb per minute (Boag, 1980).

*Rotylenchus buxophilus* is a migratory ectoparasite of roots and attacks English boxwood (*Buxus sempervirens* var. *suffruticosa* L.) in Maryland and neighbouring states of the USA. A number of other plants are attacked by it including lima beans, privet, rye and strawberry. Golden (1956) found that 250 *R. buxophilus*, when inoculated into young English boxwood, produced stunted, non-vigorous plants with considerable root damage, and in about 8 months the population increased to an average of 7300 individuals.

*Scutellonema* spp. are mostly found in the tropics and probably originated and radiated out from Africa, where they are very common on indigenous plants. In Queensland, Australia, there are some species of this genus which have much smaller scutella (e.g. *S. minutum*). Some species (*S. bradys*, *S. brachyurus*) have been distributed by man in planting materials. *Scutellonema bradys* is endoparasitic in yams in Brazil, Cuba, Guatemala, Côte d'Ivoire, Jamaica, Nigeria and Puerto Rico, and builds up large populations (maximum recorded 62,000 per 10 g of tuber), causing severe damage (dry rot) during storage (see reviews by Siddiqi, 1972b; Bridge, 1982).

*Scutellonema brachyurus* is well distributed in the tropics. It has a very wide host range of cultivated plants and is primarily an ectoparasite (see Siddiqi, 1974a). A population of 4000–5000 individuals per gal. of soil caused reduction of 57% and 43%, respectively, in top and root weights of tobacco. The optimum temperature for development of *Scutellonema* spp. is around  $24\text{--}28^{\circ}\text{C}$ , the development is retarded when the temperature is below  $15^{\circ}\text{C}$ . Like other hoplolaimids, they have a tough cuticle and can survive in dry soil for several months. *Scutellonema cavenessi* survived in dry soil kept at  $25\text{--}28^{\circ}\text{C}$  for 2 years and, upon revival, the nematodes mated and laid eggs in the absence of plants (Demeure *et al.*, 1980).

The spiral nematodes, *Helicotylenchus* spp., are cosmopolitan. They are ectoparasites of roots but may occur in the cortical tissues (*H. multicinctus*) although not migrating through the cortex. *Helicotylenchus multicinctus* is an important parasite of banana throughout the banana-growing areas of the world. The nematode reproduces by amphimixis and is known to survive without host plants for 4 months. *Helicotylenchus dihystra* is a cosmopolitan and polyphagous species (see Siddiqi, 1972a, for distribution and hosts), which can survive for several months in soil without host plants. Olive seedlings inoculated with 1000 *H. dihystra* showed 78% reduction in top weight after 6 months and retardation in the development of the lateral roots (Diab & El-Eraki, 1968). When associated with wilt bacterium, *Pseudomonas caryophylli*, the wilting of carnation was significantly increased. Similarly tomato wilting was much more severe when the nematode and *Pseudomonas solanacearum* were present together than when present alone (Libman *et al.*, 1964). On inoculated sugarcane seedlings, *H. dihystra* completed its life cycle in 35–37 days at  $23\text{--}33^{\circ}\text{C}$  (Rao & Swarup, 1976).

Geraert (1990) in his theory of evolutionary transformation of hoplolaims writes, 'If we assume that the formation of large scutella is a new Event (an apomorphic character) that happened by transformation of a *Rotylenchus* species we can easily accept Phillips' three *Scutellonema* species with small scutella as the beginning

of a transformation series. The further enlargement to the typical *Scutellonema* shapes occurred also in Australia and the genus spread over India and most of Africa. The spreading must have occurred before Pangaea split (200 million years ago). Having arrived in West Africa a new transformation happened: the scutella moved forwards, mostly erratically, but remaining in the posterior half of the body; these first *Peltamigratus* species spread all over South America where they show a considerable amount of speciation. *Aorolaimus* contains the species with a further shift so that one of the scutella is anterior to the vulva. It could be that this transfer happened at several places at the same time: e.g. in North America, in the Mediterranean area. The *Peltamigratus* transfer from Africa to South America appears to have taken place before the two continents separated 120 million years ago. The *Peltamigratus* transfer from South America to North America and the origin of the American *Aorolaimus* species must have been after the reunion of both continents. The origin of *Hoplolaimus* is less evident; it could be that *Hoplolaimus* species evolved by body enlargement from *Aorolaimus* and/or *Peltamigratus*-like ancestors. If so, it probably happened independently in several places: USA, Mediterranean area, India... In these regions both forms, with 3 and 6 oesophageal gland nuclei, occur. Only a few species with 3 gland nuclei invaded other areas, e.g. Africa.'

Two points must be made here on Geraert's theory of transformation of hoplolaims. First, it appears from the abundance and diversification of *Scutellonema* species in Africa that Phillips' (1971) three species with small scutella do not represent the beginning of the transformation of *Rotylenchus* to *Scutellonema*. *Scutellonema* must have originated in Africa and dispersed to other regions, Phillips' three species representing a separate origin in Australia, where they remained confined. Second, there are three groups of *Hoplolaimus* species which seem to have originated in different regions: (i) *Hoplolaimus*, *sensu stricto*, with tiled head bearing a round perioral disc, lateral fields with four incisures up to tail tip, excretory pore close to hemizonid and uninucleate dorsal oesophageal gland, originating in South America and spreading to North America; (ii) *Basirolaimus*, having head with irregular cuticular divisions and bearing a lemon-shaped perioral disc, lateral fields obliterated, excretory pore at a distance from the hemizonid and dorsal oesophageal gland with four nuclei, originating in the oriental region; and (iii) *Ethiolaimus* with characters similar to (ii) but having a roughly rectangular perioral disc and uninucleate dorsal oesophageal gland, originating in and being largely confined to Africa.

Hunt & Freire (1994) described *Hoplolaimus diadematus* from Brazil, which has basal lip annules inflated and its surface divided into 20 blocks, a suboval oral disc, three oesophageal gland nuclei and distinct incisures in the lateral field. On its relationship with other *Hoplolaimus sensu stricto* they commented, 'In having the basal cephalic annule divided into blocks by longitudinal striae and the dorsal oesophageal gland lobe uninucleate, this species falls into *Hoplolaimus (sensu stricto)* rather than *Basirolaimus* Shamsi, 1979. Whether *Basirolaimus* merits separate generic status is a contentious point [see Luc (1981), Siddiqi (1986) and Fortuner (1987) for opposing views], but the differences, whether considered as being of generic level or not, do appear to be consistent and are certainly of value in dividing *Hoplolaimus (sensu stricto)* into two distinct groups of species.'

*Basirolaimus* has not gained due recognition as a genus. The present solution is

its recognition as a subgenus. The taxonomy of *Hoplolaimus*, *sensu lato*, demands that three subgenera should be recognized for the species of *Hoplolaimus*, *sensu lato* – *Hoplolaimus*, *Basirolaimus* and *Ethiolaimus*. The use of subgeneric categories does help in understanding the inter-relatedness to be useful in identification, and in indicating probable lines of evolution of the species. Their use does not affect the binomen.

The subfamily Hoplolaiminae was established by Filipjev (1934) for tylenchids with strongly annulated cuticle and large stylet: *Atylenchus*, *Criconema*, *Hoplolaimus*, *Iota* (= *Hemicriconemoides*), *Paratylenchus*, *Procriconema* (= *Hemicycliophora*), the six genera being now placed in five different superfamilies. Filipjev's concept of Hoplolaiminae was that of Criconematinae since he considered the spiral nematodes to be in the Tylenchinae, and later (1936) he proposed *Rotylenchus* and *Hoplolaimus* to the Tylenchinae.

Thorne (1949) re-defined Hoplolaiminae as a subfamily of Tylenchidae and included under it, besides *Hoplolaimus*, the genera *Rotylenchus* and *Helicotylenchus*. Since Steiner (1945) established *Helicotylenchus* with *H. nannus* as type species, the differentiation of this genus from *Rotylenchus* was difficult until Golden (1956) separated the two on sound characters. Andr  ssy (1958) revised Hoplolaiminae, in which he recognized two groups, the *Hoplolaimus* group with scutellum-like, large phasmids and comprising *Hoplolaimus* and his new genus *Scutellonema*, and the *Rotylenchus* group with pore-like small phasmids containing *Rotylenchus*, *Helicotylenchus* and his new genus *Gottholdsteineria*. *Gottholdsteineria* was proposed for those species of *Rotylenchus* which have the cephalic region not set off, lateral fields not areolated on most of the body and gubernaculum lacking titillae, namely *R. goodeyi* (type species), *R. buxophilus*, *R. pararobustus* and *G. quarta*. The genus was synonymized with *Helicotylenchus* by Perry *et al.* (1959) and with *Rotylenchus* by Sher (1961). Sher (1961) emended the diagnosis of Hoplolaiminae, assigning it to the Hoplolaimidae. Hoplolaimidae as a family was accepted by Chitwood (1958) who considered it to contain the subfamilies Hoplolaiminae, Heteroderinae, Nacobbiniae and Pratylenchinae. However, in 1967, Allen & Sher once again assigned the Hoplolaiminae to the family Tylenchidae.

In Siddiqi's (1986) book, four subfamilies under Hoplolaimidae were recognized, viz. Hoplolaiminae, Aphasmatylenchinae, Rotylenchinae and Rotylenchoidinae. In the present edition of the book, Andr  ssy's (1958) concept of assigning hoplolaims to two groups based on the size and structure of the phasmid is followed: Hoplolaiminae is recognized for those genera which have scutellum-like phasmids and Rotylenchoidinae for the genera having pore-like phasmids. The subfamily Rotylenchinae is considered a junior synonym of Rotylenchoidinae.

The superfamily concept of Hoplolaimoidea was used by Paramonov (1967) who proposed the two sub-superfamily groups, Hoplolaimini (with Hoplolaimidae, Heteroderidae and Pratylenchidae) and Criconematini (with Criconematidae) under Hoplolaimoidea (the ICZN Article 35a allows for the creation of any supplementary categories in the family group, but ending -ini is reserved for an infra-subfamily name, the tribe; hence Hoplolaimini and Criconematini of Paramonov are here emended as Hoplolaimoidi and Criconematoidi, respectively). Taxonomists' opinions have been divided on the superfamily concept and on the status of Hoplolaimoidea and Heteroderoidea.

Siddiqi (1971) considered Hoplolaimidae as a family of Tylenchoidea and as comprising the subfamilies Hoplolaiminae, Hoplotylinae, Rotylenchoidinae and Rotylenchulinae. Golden (1971) also recognized Hoplolaimidae as belonging to Tylenchoidea but his composition of the family was different. He considered Hoplolaiminae, Aphasmatylenchinae, Rotylenchinae (as a new subfamily) and Rotylenchoidinae under Hoplolaimidae while Rotylenchulinae was newly assigned to the family Nacobbidae which was placed under Heteroderoidea. Both Hoplolaimoidea and Heteroderoidea were recognized by Siddiqi (1980).

Siddiqi's (1980) concept of the Hoplolaimoidea (heteroderids excluded) was based on the presence of a strong stylet, cephalic framework and median oesophageal bulb, didelphy and phasmids usually located on or near the tail. He traced the possible evolution of the Hoplolaimoidea from the ancient didelphic Psilenchinae–Leipotylenchinae–Antarctenchinae complex.

In this book, the Tylenchoidea are recognized as a superfamily characterized by the phasmid-like structures, the prophasms, located just dorsal to the lateral field in the postmedian region of the body, in the female near the vulva, monodelphy and by the absence of the phasmids and is assigned to Tylenchata of Tylenchina. Hoplolaimoidea is reconstituted here as a group of advanced root parasites which have enlarged subventral oesophageal glands, almost always extending past the dorsal gland. The group includes the families Heteroderidae and Meloidogynidae. The enlargement of the subventral oesophageal gland normally occurs in the pre-parasitic females of Hexatylinina to enable them to penetrate the insect cuticle. Apparently this condition of the oesophageal glands has led Hoplolaimoidea to become parasites of deep root tissues, in four major ways, i.e. as migratory ectoparasites which sometimes may become completely embedded in the roots (Hoplolaimidae), as migratory endoparasites (Pratylenchidae), as sedentary semi-ectoparasites (Rotylenchulidae) and as sedentary endoparasites (Meloidogynidae, Heteroderidae).

### **Family Hoplolaimidae Filipjev, 1934 (Wieser, 1953)**

**syn. Nemonchidae Skarbilovich, 1959**

**Aphasmatylenchidae Sher, 1965 (Fotadar & Handoo, 1978)**

**Pararotylenchidae Baldwin & Bell, 1981 (Eroshenko, 1984)**

**Interrotylenchidae Eroshenko, 1984**

#### **Diagnosis**

Hoplolaimoidea. Small to moderately large (usually 0.6–1.5 mm); generally vermiform. Sexual dimorphism manifest in cephalic region. Lateral fields each with four incisures, rarely reduced or absent (e.g. *Basirolaimus*). Deirids absent. Phasmids either small, with pore-like apertures near or a little anterior to anus or **large scutellum-like, near anus or much anterior to it** anywhere on body behind oesophageal region; absent in *Aphasmatylenchus*. **Cephalic region elevated, high arched**, framework strongly sclerotized, dorsal and ventral arms may appear bifid or trifid posteriorly; labial disc usually distinct; labial sensilla not on surface (except *Pararotylenchus*). Oesophageal glands overlapping intestine (except *Pararotylenchus*); subventral glands symmetrical in size and location (except *Antarctylus*). Ovaries paired or rarely

single. Female tail short, rounded (about one body width or less long), or conical (over two anal body widths, e.g. *Antarctylus*) with protoplasmic portion less than two body widths long and a distinct hyaline terminal portion. Male tail short (except *Aphasmatylenchus*). **Bursa large, enveloping tail**; flaps crenate, sometimes indented at tip, **usually lacking phasmidial pseudoribs**. Spicules robust or slender, straight to arcuate, with distal flanges which may be reduced. Gubernaculum large, protrusible or fixed; telamon (= capitulum) present or absent.

#### Type subfamily

Hoplolaiminae Filipjev, 1934

#### Other subfamilies

Aphasmatylenchinae Sher, 1965

Rotylenchoidinae Whitehead, 1958

#### Remarks

Aphasmatylenchidae Sher, 1965 (Fotedar & Handoo, 1978) is here recognized at subfamily rank while Pararotylenchidae Baldwin & Bell, 1981 (Eroshenko, 1984) and Interrotylenchidae Eroshenko, 1984 are considered as synonyms of Hoplolaimidae because their type genera are synonyms of *Rotylenchus*, a member of Hoplolaimidae (see discussion by Maggenti *et al.*, 1988). Members of Rotylenchinae and Rotylenchoidinae are grouped here under one subfamily, the Rotylenchoidinae.

#### Key to subfamilies of Hoplolaimidae

1. Phasmids present ..... 2  
     Phasmids absent ..... **Aphasmatylenchinae**
2. Phasmids large, scutellum-like ..... **Hoplolaiminae**  
     Phasmids small, pore-like ..... **Rotylenchoidinae**

### Subfamily Hoplolaiminae Filipjev, 1934

#### Diagnosis

Hoplolaimidae. **Cephalic region usually offset, first and basal annules marked with longitudinal indentations**. Lateral fields with four incisures, sometimes reduced or absent (*Basirolaimus*, *Ethiolaimus*, *Peltamigratus*). **Phasmids enlarged, scutellum-like, near anus or aberrantly placed on body**. Stylet robust, knobs compact tulip-shaped or rounded. Dorsal oesophageal gland orifice about one-fourth or less stylet length behind stylet base. Didelphic, amphidelphic; ovaries paired, outstretched. Epiptygma often distinct. Female tail short, rounded. Spicules robust, usually flanged distally. Gubernaculum also robust, usually protrusible and with telamon.

#### Type genus

(Subsequent designation by Thorne, 1949)

*Hoplolaimus* Daday, 1905

## Other genera

*Aorolaimus* Sher, 1963*Peltamigratus* Sher, 1964*Scutellonema* Andr ssy, 1958**Key to genera of Hoplolaiminae**

1. Stylet knobs tulip-shaped, each with one to three anteriorly directed tooth-like projections ..... *Hoplolaimus*  
     Stylet knobs not tulip-shaped, without tooth-like projections ..... 2
2. Scutella in or near anal region, close to or opposite each other ..... *Scutellonema*  
     Scutella much anterior to anus, separated from each other ..... 3
3. One scutellum prevulval, another postvulval ..... *Aorolaimus*  
     Both scutella postvulval ..... *Peltamigratus*

**Genus *Hoplolaimus* Daday, 1905**syn. *Nemonchus* Cobb, 1913*Hoplolaimoides* Shakil, 1973*Basirolaimus* Shamsi, 1979*Ethiolaimus* gen. n.

## Diagnosis

Hoplolaiminae. Large-sized (1–2 mm). Lateral field usually with two or four incisures, sometimes obliterated. Cephalic region offset, rounded, marked by prominent transverse and longitudinal striae; **labial disc distinct; basal annule marked by more than six longitudinal striae**; framework very heavily sclerotized. **Stylet massive, with compact tulip-shaped basal knobs** having one to three anterior tooth-like projections. **Excretory pore near hemizonid or more anterior**. Epitygma present, often indistinct. Oesophageal glands large, overlapping intestine dorsally and laterally; dorsal gland uni- or quadrinucleate. Phasmids large, scutellum-like, not opposite each other, one prevulval, another postvulval (except *H. californicus* in which both phasmids are postvulval). Female tail hemispherical, annulated. Spicules massive, somewhat cylindroid, may be dimorphic with distal flanges variable in size. Gubernaculum large, protrusible, with titillae and telamon.

## Type subgenus

*Hoplolaimus* Daday, 1905

## Other subgenera

*Basirolaimus* Shamsi, 1979*Ethiolaimus* subgen. n.**Key to subgenera of *Hoplolaimus***

1. Lateral field with four incisures, not obliterated; excretory pore usually closely behind hemizonid; labial disc rounded ..... *Hoplolaimus*  
     Lateral field with one to three incisures, obliterated; excretory pore anterior to hemizonid; labial disc lemon- to spindle-shaped ..... 2



2. Dorsal oesophageal gland uninucleate ..... *Ethiolaimus*  
     Dorsal oesophageal gland quadrinucleate ..... *Basirolaimus*

### Subgenus *Hoplolaimus* Daday, 1905

(Figs 8(b)D; 11, A; 57, A–G)

#### Diagnosis

Genus *Hoplolaimus*. **Lateral field distinct, with four incisures**, outer bands often areolated. Cephalic basal annule divided into minute squares; **labial disc rounded**; lateral lip sectors generally as large as submedians, not extending on lateral sides of cephalic region. Excretory pore closely behind hemizonid. Dorsal oesophageal gland uninucleate.

#### Type species

*Hoplolaimus tylenchiformis* Daday, 1905

#### Present status

*Hoplolaimus* (*Hoplolaimus*) *tylenchiformis* Daday, 1905  
     syn. *Criconema tylenchiforme* (Daday) Micoletzky, 1917

#### Other species

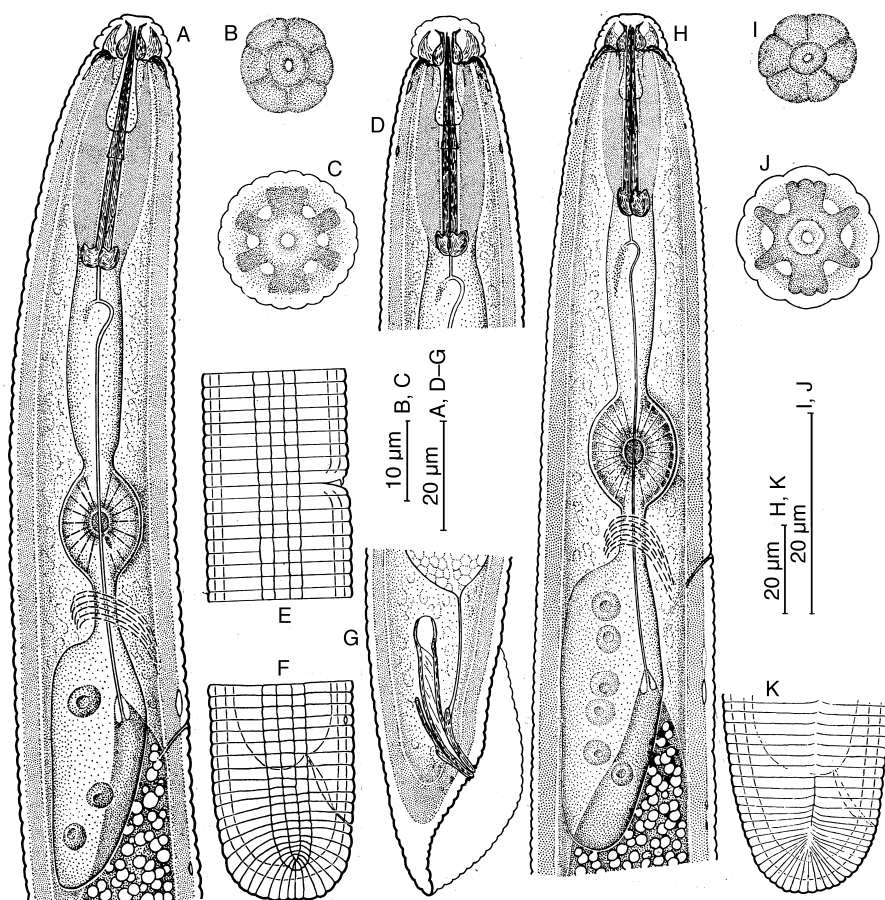
*Hoplolaimus* (*Hoplolaimus*) *aorolaimoides* Siddiqi, 1972  
*H.* (*H.*) *californicus* Sher, 1963  
     syn. *Hoplolaimoides californicus* (Sher) Shakil, 1973  
*H.* (*H.*) *concaudajuwencus* Golden & Minton, 1970  
*H.* (*H.*) *galeatus* (Cobb, 1913) Thorne, 1935  
     syn. *Nemonchus galeatus* Cobb, 1913  
     *Hoplolaimus coronatus* Cobb, 1923  
*H.* (*H.*) *igualaensis* Cid del Prado V., 1994  
*H.* (*H.*) *imphalensis* Khan & Khan, 1985  
*H.* (*H.*) *intermedius* (Suryawanshi) Baujard, Castillo, Doucet, Martiny, Mounport & N'Diaye, 1991  
     syn. *Aorolaimus intermedius* Suryawanshi, 1971  
*H.* (*H.*) *magnistylus* Robbins, 1982  
*H.* (*H.*) *stephanus* Sher, 1963

#### Nomina nuda

*Hoplolaimus gadsdenensis* Thames in Sher, 1963  
*Hoplolaimus neocoronatus* Whitten in Sher, 1961

#### Remarks

*Hoplolaimoides* Shakil, 1973 (type species: *H. californicus* (Sher, 1963)), based on the location of both the phasmids in the postvulval region, has been synonymized with *Hoplolaimus*. Andr  ssy (1958) studied the original female (holotype) of *H. tylenchiformis* Daday and synonymized *H. coronatus* Cobb with it. Sher (1961) regarded *H. coronatus* as a synonym of *H. galeatus*. *Hoplolaimus uniformis* Thorne was synonymized with *Rotylenchus robustus* de Man by Loof & Oostenbrink (1958).



**Fig. 57.** A–G. *Hoplolaimus* (*Hoplolaimus*) *tylenchiformis* Daday. H–K. *Hoplolaimus* (*Basirolaimus*) *seinhorsti* Luc. A and H. Oesophageal regions of females. B and I. *En face* views of females. C and J. Cross-sections through basal annule of head of females. D and G. Head and tail end of male, respectively. E. Surface view at vulval region. F and K. Tail ends of females showing lateral field. (After Sher (1963), courtesy *Nematologica*.)

**ETYMOLOGY.** From Greek *hoplo* = arming, and *laimos* = throat.

*Hoplolaimus tylenchiformis* was collected by Daday (1905) from a mud-hole on Banco Island in the Paraguay River at Asuncion, Paraguay. *Hoplolaimus* spp. mostly occur in the New World. A key to *Hoplolaimus* spp. is given by Handoo and Golden (1992).

**Subgenus *Basirolaimus* Shamsi, 1979, (grad. n.)**

(Figs 57, H–K; 58, C–F)

**Diagnosis**

Genus *Hoplolaimus*. **Lateral field** with one to three incisures, **obliterated**. Cephalic region annules with six longitudinal grooves, basal annule not divided into minute squares; labial disc lemon- or spindle-shaped; lateral lip sectors narrower than sub-medians, extending on lateral sides of cephalic region; cephalic framework with six equal sectors. **Excretory pore a few annules anterior to hemizonid**. **Dorsal oesophageal gland quadrinucleate**.

**Type species**

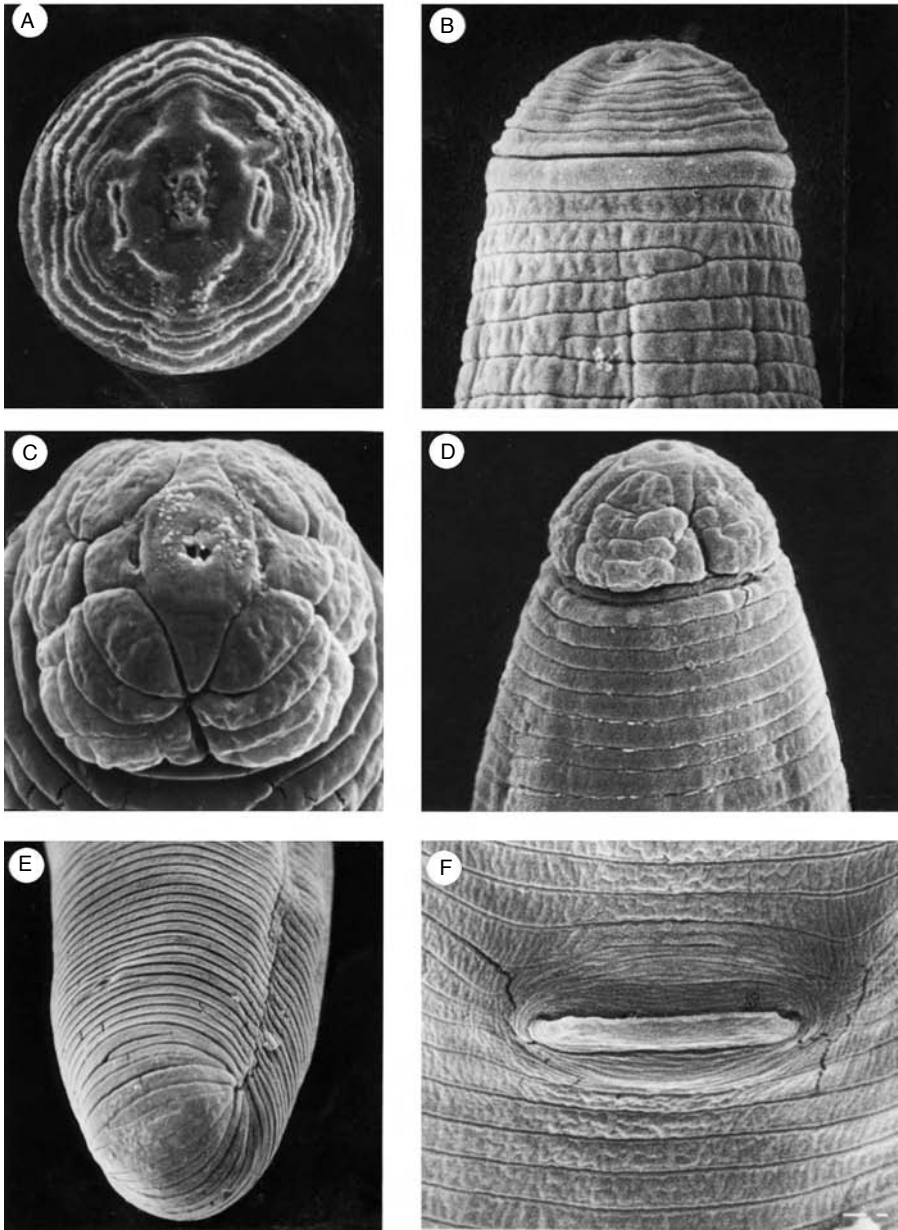
*Basirolaimus seinhorsti* (Luc, 1958) Shamsi, 1979

**Present status**

*Hoplolaimus* (*Basirolaimus*) *seinhorsti* Luc, 1958  
 syn. *Hoplolaimus seinhorsti* Luc, 1958  
*Basirolaimus seinhorsti* (Luc) Shamsi, 1979  
*Hoplolaimus sheri* Suryawanshi, 1971  
*Basirolaimus sheri* (Suryawanshi) Siddiqi, 1986

**Other species**

*Hoplolaimus* (*Basirolaimus*) *abelmoschi* Tandon & Singh, 1973\*  
 syn. *Hoplolaimus abelmoschi* Tandon & Singh, 1973  
*Basirolaimus abelmoschi* (Tandon & Singh) Siddiqi, 1986  
*H. (B.) aegypti* Shafiee & Koura, 1969  
 syn. *Hoplolaimus aegypti* Shafiee & Koura, 1969  
*Basirolaimus aegypti* (Shafiee & Koura) Shamsi, 1979  
*H. (B.) cephalus* Mulk & Jairajpuri, 1976\*  
 syn. *Hoplolaimus cephalus* Mulk & Jairajpuri, 1976  
*Basirolaimus cephalus* (Mulk & Jairajpuri) Shamsi, 1979  
*H. (B.) chambus* Jairajpuri & Baqri, 1973  
 syn. *Hoplolaimus chambus* Jairajpuri & Baqri, 1973  
*Basirolaimus chambus* (Jairajpuri & Baqri) Siddiqi, 1986  
*H. (B.) citri* (Khan & Khan, 1985) Ebsary, 1991\*  
*Basirolaimus citri* Khan & Khan, 1985  
*Hoplolaimus citri* (Khan & Khan) Ebsary, 1991  
*H. (B.) clarissimus* Fortuner, 1973  
 syn. *Hoplolaimus clarissimus* Fortuner, 1973  
*Basirolaimus clarissimus* (Fortuner) Shamsi, 1979  
*H. (B.) columbus* Sher, 1963  
 syn. *Hoplolaimus columbus* Sher, 1963  
*Basirolaimus columbus* (Sher) Shamsi, 1979  
*H. (B.) dimorphicus* Mulk & Jairajpuri, 1976\*  
 syn. *Hoplolaimus dimorphicus* Mulk & Jairajpuri, 1976  
*Basirolaimus dimorphicus* (Mulk & Jairajpuri) Shamsi, 1979  
*H. (B.) dubius* Chaturvedi & Khera, 1979\*



**Fig. 58.** Scanning electron micrographs. A and B. *Hirschmanniella mucronata* (Das), female from India, face and lateral view of head of female, respectively. C–F. *Hoplolaimus* (*Basirolaimus*) *seinhorsti* Luc, females from Tanzania. C and D. Face and lateral view of head of female, respectively. E. Tail of female, subventral view. F. Vulva and epiptygma.

- syn. *Hoplolaimus dubius* Chaturvedi & Khera, 1979  
*Basirolaimus dubius* (Chaturvedi & Khera) Siddiqi, 1986
- H. (B.) indicus* Sher, 1963  
 syn. *Hoplolaimus indicus* Sher, 1963  
*Basirolaimus indicus* (Sher) Shamsi, 1979  
*Hoplolaimus arachidis* Maharaju & Das, 1982  
*Basirolaimus arachidis* (Maharaju & Das) Siddiqi, 1986
- H. (B.) jalalabadiensis* (Khan & Khan, 1985) Ebsary, 1991\*  
 syn. *Basirolaimus jalalabadiensis* Khan & Khan, 1985  
*Hoplolaimus jalalabadiensis* (Khan & Khan) Ebsary, 1991
- H. (B.) maggentii* Cid del Prado V., 1994  
 syn. *Hoplolaimus maggentii* Cid del Prado V., 1994  
*Basirolaimus maggentii* (Cid del Prado V., 1994) comb. n.
- H. (B.) puertoricensis* Ramirez, 1964  
 syn. *Hoplolaimus puertoricensis* Ramirez, 1964  
*Basirolaimus puertoricensis* (Ramirez) Siddiqi, 1986
- H. (B.) sacchari* (Shamsi, 1979) Luc, 1981\*  
 syn. *Basirolaimus sacchari* Shamsi, 1979  
*Hoplolaimus sacchari* (Shamsi) Luc, 1981
- H. (B.) seshadrii* Mulk & Jairajpuri, 1976\*  
 syn. *Hoplolaimus seshadrii* Mulk & Jairajpuri, 1976  
*Basirolaimus seshadrii* (Mulk & Jairajpuri) Shamsi, 1979
- H. (B.) singhi* Das & Shivaswamy, 1977\*  
 syn. *Hoplolaimus singhi* Das & Shivaswamy, 1977  
*Basirolaimus singhi* (Das & Shivaswamy) Siddiqi, 1986
- H. (B.) tabacum* Firoza, Nasira & Maqbool, 1990\*  
 syn. *Hoplolaimus tabacum* Firoza, Nasira & Maqbool, 1990  
*Basirolaimus tabacum* (Firoza, Nasira & Maqbool, 1990) comb. n.

### Species inquirendae

- Hoplolaimus steineri* Kannan, 1961 (? senior syn. *H. (B.) indicus*)  
*Hoplolaimus jonesi* Kumar, 1981  
*Hoplolaimus sanwali* Kumar, 1981

### Remarks

Luc (1981) synonymized *Basirolaimus* with *Hoplolaimus* stating that the presence of six oesophageal gland nuclei is not a primary characteristic as it involves a simple duplication of the original number and that it can be considered as an intra-generic variation in the genus *Hoplolaimus*. The six gland nuclei are the result not of duplication of the original three nuclei, but of the occurrence of four similar-sized nuclei in the dorsal gland instead of one. The report of five nuclei in some species is an error since one of the two subventral gland nuclei is easily overlooked as the two are not in the same optical level. The occurrence of four nuclei in the dorsal gland of *Basirolaimus* spp. is a unique character of the Tylenchida though seven oesophageal gland nuclei of the same size have been reported in *Rotylenchus magnus magnus* and *R. m. jaeni* (Luc, 1995) but there is no evidence of four dorsal gland nucleus in these species. This, supplemented with the characters of the head and labial disc, lateral

field, excretory pore position relative to hemizonid and geographical distribution, differentiates *Basirolaimus* from *Hoplolaimus*.

A large number of species of *Hoplolaimus* (*Basirolaimus*) have been described from South Asia. Those marked with (\*) need further study to establish their identity since many of them are similar either to *H. (B.) seinhorsti* or *H. (B.) indicus*.

ETYMOLOGY. Commemorative name honouring M.A. Basir; and suffix of *Hoplolaimus* to show the derivation of the genus by splitting *Hoplolaimus*. The creation of such compound names with awkward meanings should be discouraged.

The type species was described from around the roots of cotton (*Gossypium hirsutum* L.) at Miary, near Tulear, Malagasy. *Basirolaimus* spp. mostly occur in the Old World; *B. columbus* is also found in the New World (USA).

### Subgenus *Ethiolaimus* subgen. n.

(Figs 59, A; 60, A–E)

#### Diagnosis

Genus *Hoplolaimus*. **Lateral field obliterated** or with two incisures. Cephalic region annules with six longitudinal grooves, basal annule divided into squares or rectangular blocks; labial disc lemon- or spindle-shaped. Excretory pore a few annules anterior to hemizonid. Dorsal oesophageal gland uninucleate. Geographical distribution mostly in the Ethiopian region.

#### Type species

*Ethiolaimus pararobustus* (Schuurmans Stekhoven & Teunissen, 1938) Sher in Coomans, 1963, comb. n.

#### Present status

*Hoplolaimus (Ethiolaimus) pararobustus* (Schuurmans Stekhoven & Teunissen, 1938) Sher in Coomans, 1963

syn. *Tylenchorhynchus pararobustus* Schuurmans Stekhoven & Teunissen, 1938

*Rotylenchus pararobustus* (Schuurmans Stekhoven & Teunissen) Filipjev & Schuurmans Stekhoven, 1941

*Gottholdsteineria pararobusta* (Schuurmans Stekhoven & Teunissen) Andrassy, 1958

*Hoplolaimus pararobustus* (Schuurmans Stekhoven & Teunissen) Sher, 1963

*Ethiolaimus pararobustus* (Schuurmans Stekhoven & Teunissen) comb. n.

*Hoplolaimus proporicus* Goodey, 1957

*Hoplolaimus angustalatus* Whitehead, 1959

*Hoplolaimus kittenbergeri* Andrassy, 1961

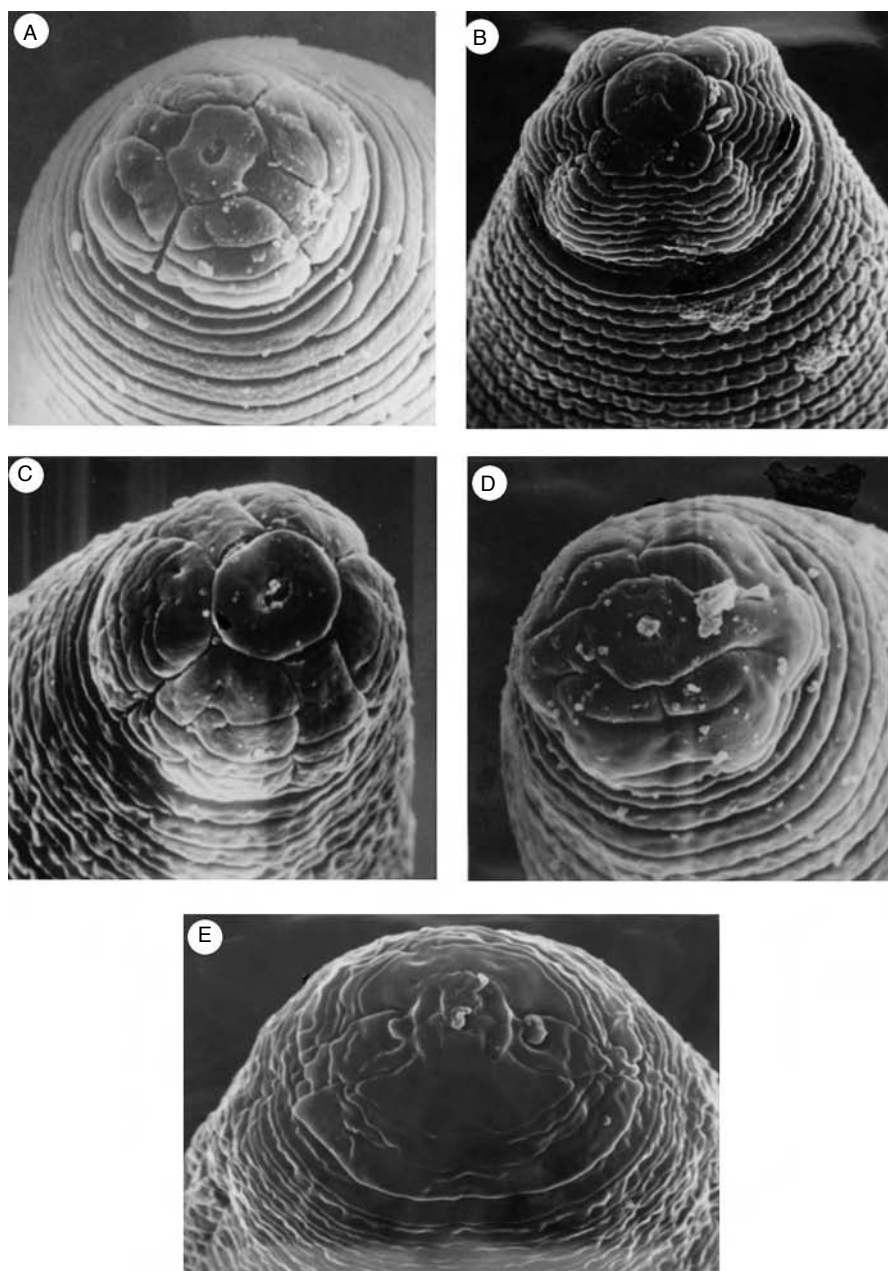
#### Other species

*Hoplolaimus (Ethiolaimus) capensis* Van den Berg & Heyns, 1970

syn. *Hoplolaimus capensis* Van den Berg & Heyns, 1970

*Ethiolaimus capensis* (Van den Berg & Heyns, 1970) comb. n.

*H. (E.) casparus* Van den Berg & Heyns, 1970



**Fig. 59.** Scanning electron micrographs of *en face* views of females. A. *Hoplolaimus* (*Ethiolaimus*) *pararobustus*. B. *Aphasmatylenchus straturatus*. C. *Peltamigratus* (*Nectopelta*) *longistylus*. D. *Peltamigratus* (*Peltamigratus*) *macbethi*. E. *Radopholus similis*. (Courtesy P. Baujard, Muséum National d'Histoire Naturelle, Paris.)

- syn. *Hoplolaimus casparus* Van den Berg & Heyns, 1970  
*Ethiolaimus casparus* (Van den Berg & Heyns, 1970) comb. n.  
*H. (E.) diadematus* Hunt & Freire, 1994  
 syn. *Hoplolaimus diadematus* Hunt & Freire, 1994  
*Ethiolaimus diadematus* (Hunt & Freire, 1994) comb. n.

ETYMOLOGY. Generic name is derived from L. *Aethiopia* = Africa, and suffix of *Hoplolaimus*.

The type species, *H. (Ethiolaimus) pararobustus* is a species complex and is widely distributed in Africa.

### Genus *Aorolaimus* Sher, 1963

(Fig. 60, F–J)

#### Diagnosis

Hoplolaiminae. Small to moderately large (0.7–1.2 mm), arcuate to spiral upon relaxation. Lateral fields prominent, each with four incisures, not areolated except in oesophageal region and at phasmids. **Phasmids (scutella), one pre-, another postvulval.** Cephalic region offset or continuous, with or without longitudinal striae; lateral lip sectors not elongated; framework not as massive as in *Hoplolaimus*. Stylet knobs rounded, **devoid of anterior tooth-like projections.** Oesophageal glands large, uninucleate, overlapping intestine dorsally and laterally. Excretory pore behind hemizonid. Epiptygma indistinct. Female tail hemispheroidal, annulated. Spicules and gubernaculum not massive.

#### Type species

*Aorolaimus helicus* Sher, 1963

#### Other species

- Aorolaimus baldus* Thorne & Malek, 1968  
*A. capsici* Jiménez Millán, Arias Delgado & Fijo, 1964  
*A. leiomerus* (de Guiran, 1963) de Guiran & Sher, 1969  
 syn. *Hoplolaimus leiomerus* de Guiran, 1963  
*Aorolaimus israeli* Sher, 1963  
*A. leipogrammus* Sher, 1963  
*A. mexicanensis* Cid del Prado V., 1994  
*A. torpidus* Thorne & Malek, 1968  
*(A. superbus* in Thorne & Malek, 1968 = *lapsus calami*)

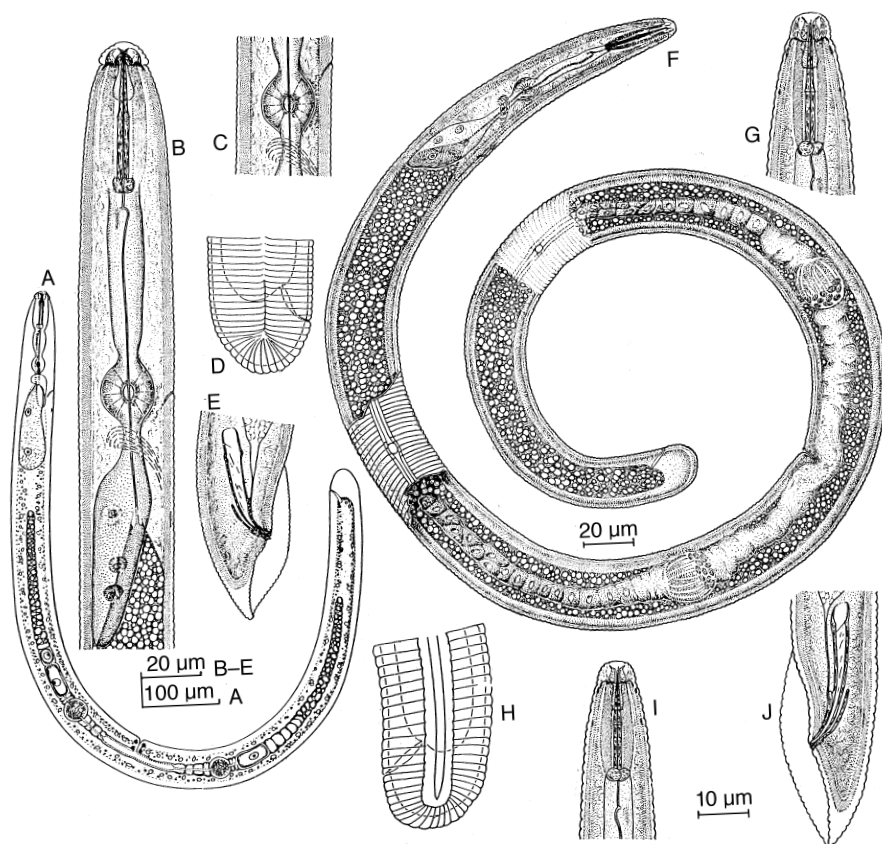
#### Note

Baujard *et al.* (1994) considered *Aorolaimus* synonymous with *Peltamigratus*, *A. thornei* as a junior synonym of *A. pachyurus* and *A. brevicaudatus*, *A. conicori* and *A. triticeus* as junior synonyms of *A. longistylus*. They gave a key to species of *Aorolaimus*, *sensu lato*.

ETYMOLOGY. Greek *aor* = sword, and *laimos* = throat.

The type species was found on roots of rose (*Rosa* sp.) at Beltsville, Maryland, USA.





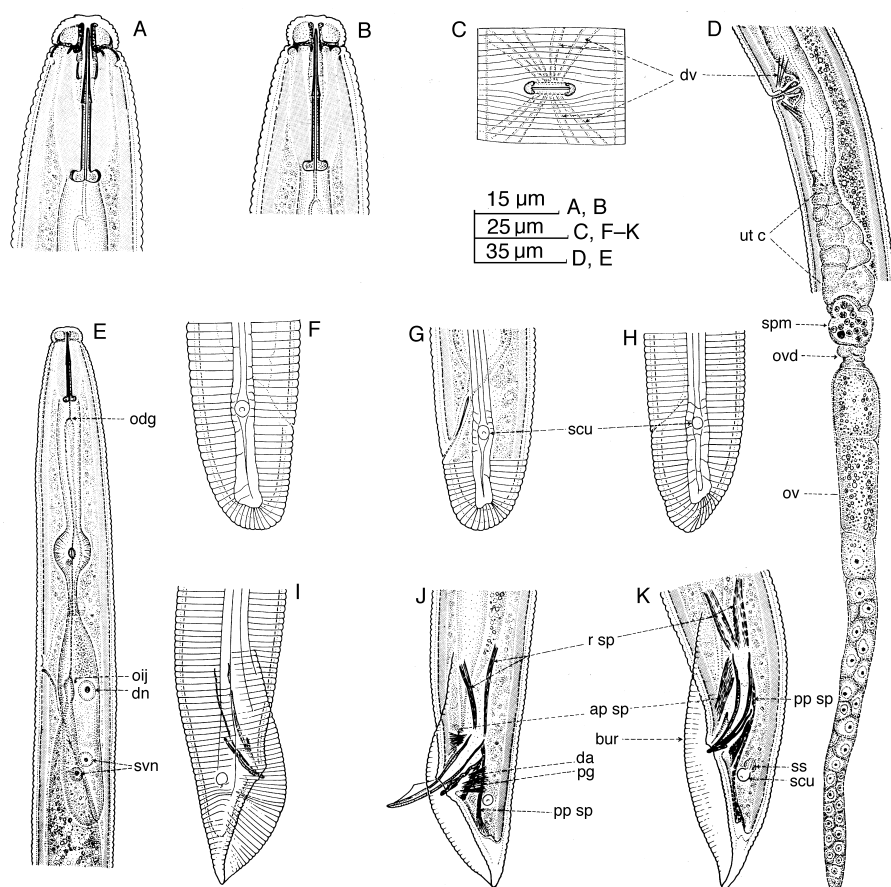
**Fig. 60.** A–E. *Hoplolaimus (Ethiolaimus) pararobustus* (Schuurmans Stekhoven & Teunissen). F–J. *Aorolaimus helicus* Sher. A and F. Females. B. Oesophageal region of female. C. Median oesophageal bulb and excretory pore. D and E. Female and male tail, respectively. G and H. Head and tail end of female, respectively. I and J. Head and tail end of male, respectively. (After Sher (1963), courtesy *Nematologica*.)

### Genus *Scutellonema* Andr  ssy, 1958

(Fig. 61)

#### Diagnosis

Hoplolaiminae. Small to moderately large (0.5–1.3 mm). Lateral fields distinct, each with four incisures, areolated only anteriorly and usually at phasmids. **Phasmids enlarged, scutellum-like, located opposite or nearly opposite each other in or close to anal region.** Cephalic region offset or continuous, annulated or smooth, with or without indentation of basal annule; lateral lip sectors usually not elongated. Stylet of medium strength; knobs round to anteriorly cupped. Oesophageal glands forming short to large overlap on intestine dorsally and laterally. Epiptygma distinct or indistinct. Female tail short rounded or dorsally convex-conoid, without terminal mucro. Bursa enveloping tail, usually not indented.



**Fig. 61.** *Scutellonema bradys* (Steiner & LeHew). A–H. Syntypes. I–K. From Nigerian yam. B, I–K. males, remainder females. A and B. Head ends. C. Vulval region. D. Posterior gonad. E. Oesophageal region. F–K. Tail ends. Ap sp, anterior protractor of spicule; bur, bursa; da, dilators of anus; dn, dorsal gland nucleus; dv, dilators of vulva; odg, orifice of dorsal oesophageal gland; oij, oesophago-intestinal junction; ov, ovary; ovd, oviduct; pg, protractor of gubernaculum; pp sp, posterior protractor of spicule; r sp, retractors of spicule; scu, scutellum; spm, spermatheca; ss, sensilla sac; svn, subventral gland nucleus; ut c, uterine columella. (After Siddiqi, 1972b.)

### Type species

*Scutellonema blaberum* (Steiner, 1937) Andr ssy, 1958

### Present status

*Scutellonema bradys* (Steiner & LeHew, 1933) Andr ssy, 1958

syn. *Hoplolaimus bradys* Steiner & LeHew, 1933

*Anguillulina bradys* (Steiner & LeHew) Goodey, 1935

*Rotylenchus bradys* (Steiner & LeHew) Filipjev, 1936

*Rotylenchus blaberus* Steiner, 1937

*Scutellonema blaberum* (Steiner, 1937) Andrásy, 1958  
*Scutellonema dioscoreae* Lordello, 1959

### Other species

- Scutellonema africanum* Smit, 1971
- S. anisomeristum* Siddiqi & Bridge, 1991
- S. bangaloreense* Khan & Nanjappa, 1972
- S. bizanae* Van den Berg & Heyns, 1973
  - syn. *Scutellonema multistriatum* Van den Berg & Heyns, 1981
- S. brachyurus* (Steiner, 1938) Andrásy, 1958
  - syn. *Rotylenchus brachyurus* Steiner, 1938
  - Rotylenchus coheni* Goodey, 1952
  - Scutellonema coheni* (Goodey) Andrásy, 1958
  - Rotylenchus boocki* Lordello, 1957
  - Scutellonema boocki* (Lordello) Andrásy, 1958
  - Scutellonema orientale* Rashid & Khan, 1974
  - Scutellonema ramai* Verma, 1972
  - Scutellonema sheri* Edward & Rai, 1970
- S. brevistyletum* Siddiqi, 1972
- S. cavenessi* Sher, 1964
- S. cephalidium* Anderson, Handoo & Townshend, 1984
- S. chen* Peng & Siddiqi, 1994
- S. clariceps* Phillips, 1971
- S. clathricaudatum* Whitehead, 1959
  - syn. *Hoplolaimus aberrans* Whitehead, 1960
  - Scutellonema aberrans* (Whitehead) Sher, 1961
- S. commune* Van den Berg & Heyns, 1973
- S. conicaudatum* Sivakumar & Selvasakaran, 1982
- S. conicephalus* Sivakumar & Selvasakaran, 1982
- S. dentivagina* Van den Berg & Heyns, 1973 (original spelling *dentivaginum*)
- S. dreyeri* Van den Berg & De Waele, 1990
- S. erectum* Sivakumar & Khan, 1981
- S. grande* Sher, 1964
  - syn. *Scutellonema mangiferae* Khan & Basir, 1965
  - Scutellonema eclipsi* Ganguly & Khan, 1983
- S. impar* Phillips, 1971
  - syn. *Rotylenchus impar* (Phillips) Germani, Baldwin, Bell & Wu, 1986
- S. imphalum* Sultan & Jairajpuri, 1979
- S. incisicaudatum* Phillips, 1971
  - syn. *Rotylenchus incisicaudatus* (Phillips) Germani, Baldwin, Bell & Wu, 1986
- S. insulare* Phillips, 1971
  - syn. *Rotylenchus insularis* (Phillips) Germani, Baldwin, Bell & Wu, 1986
- S. labiatum* Siddiqi, 1972
- S. laeviflexum* Phillips, 1971
  - syn. *Rotylenchus laeviflexus* (Phillips) Germani, Baldwin, Bell & Wu, 1986
- S. mabelei* Van den Berg & De Waele, 1990
- S. magniphasma* Sher, 1964 (original spelling *magniphasmum*)
  - syn. *Scutellonema naveenum* Sivakumar & Khan, 1981

- S. megascutatum* Peng & Siddiqi, 1994  
*S. minutum* Sher, 1964  
*S. nigermontanum* Van den Berg, 1990  
*S. paludosum* Peng & Hunt, 1995  
*S. paralabiatum* Siddiqi & Sharma, 1994  
*S. propeltatum* Siddiqi & Sharma, 1994  
*S. sacchari* Rashid, Singh, Misra & Farooqi, 1985  
*S. sanwali* Lal, 1995  
*S. siamense* Timm, 1965  
*S. sibrium* Siddiqi & Bridge, 1991  
*S. sofiae* Van den Berg & Heyns, 1973  
*S. sorghi* Van den Berg & De Waele, 1990  
*S. transvaalense* Van den Berg, 1981  
*S. truncatum* Sher, 1964  
     syn. *Plesiorotylenchus truncatus* (Sher, 1964) Baujard, 1994  
*S. tsiksikamense* Van den Berg, 1976  
*S. unum* Sher, 1964  
*S. ussuriense* Eroshenko & Kazachenko, 1984  
*S. validum* Sher, 1964

#### Species inquirendae

- Scutellonema brabanum* Khan, Saha & Chawla, 1981  
*S. vietnamiense* Eroshenko & Tkhan, 1981

#### Species incertae sedis

- Scutellonema amabile* Eroshenko & Tkhan, 1981

ETYMOLOGY. From Latin *scutellum* (diminutive of *scutum*) = shield, for enlarged shield-like phasmids, and *nema* = nematode. Andr ssy (1958) used *scutella* as the plural of *scutellum*; the use of *scutella* as singular and *scutellae* as plural should be discouraged.

The type species was collected from yam (*Dioscorea* sp.) from Jamaica intercepted at Philadelphia, Pennsylvania, USA. A key to species is given by Germani *et al.* (1986).

### Genus *Peltamigratus* Sher, 1964

#### Diagnosis

Hoplolaiminae. Small-sized (0.6–1 mm). Lateral fields each with four incisures or posteriorly indistinct with only two inner incisures, with or without areolation in phasmid region. **Cephalic region rounded, smooth or finely annulated; longitudinal indentations present or absent;** labial disc indistinct; lateral lip sectors generally elongated. Cephalic framework heavily sclerotized. Stylet well developed, knobs rounded. Oesophageal glands large, overlapping intestine dorsally and sublaterally. **Phasmids large, scutellum-like, located in posterior part of body but much anterior to anus, at different levels, rarely opposite each other.** Epitygma distinct or indistinct. Female tail short, hemispherical or slightly tapering, usually annulated to

terminus, terminal annule may occasionally be large. Male with large bursa, generally indented terminally.

#### Type subgenus

*Peltamigratus* Sher, 1964

#### Other subgenus

*Nectopelta* Siddiqi, 1986

#### Note

F.A. Khan (1972) published the description of *Peltamigratus indicus* in an abstract and compared it with related species. The name thus becomes available. Later, in 1973, the same author and S.I. Husain published a full description of it but called it n. sp. The latter name is thus an objective synonym of the former *P. indicus*. A key to *Peltamigratus* spp. is given by Doucet (1984).

ETYMOLOGY. From Latin *pelta* = small shield (for phasmid), and *migratio* = migration.

The type species was found associated with the roots of Bermuda grass (*Cynodon dactylon*) and spotted spurge weed (Euphorbiaceae) at Sarasota, Florida, USA. It also occurs on *Cerothamnus* sp., *Crinum americanum*, *Hibiscus cannabinus*, *Paspalum* sp., *Quercus* sp. and *Sobal* spp. in Florida, USA (Sher, 1964). A key to *Peltamigratus* spp. is given by Bittencourt and Huang (1986).

#### Key to subgenera of *Peltamigratus*

1. Cephalic region distinctly annulated; lateral field in tail region with four incisures and in phasmid region areolated ..... *Nectopelta*
- Cephalic region smooth; lateral field in tail region with two incisures and in phasmid region not areolated ..... *Peltamigratus*

#### Subgenus *Peltamigratus* Sher, 1964

(Figs 59, D; 62, A–H)

#### Diagnosis

Genus *Peltamigratus*. With the characters of the genus *Peltamigratus*. Small-sized (0.6–1 mm). Lateral fields in posterior region often indistinct and with only two inner incisures, **without areolation in phasmid region. Cephalic region with indistinct or no annulation; longitudinal indentations faint or absent.** Male with large bursa, generally indented terminally.

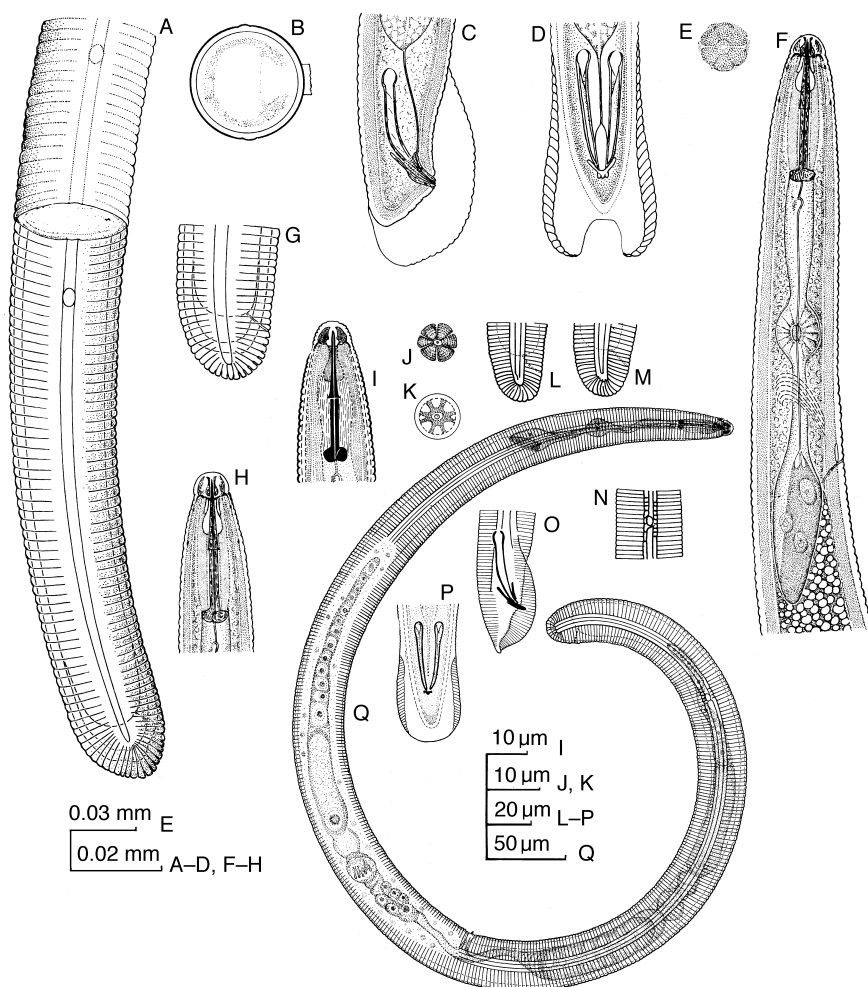
#### Type species

*Peltamigratus christiei* (Golden & Taylor, 1956) Sher, 1964

syn. *Rotylenchus christiei* Golden & Taylor, 1956

*Scutellonema christiei* (Golden & Taylor) Andrassy, 1958

*Aorolaimus christiei* (Golden & Taylor) Baujard, Castillo, Doucet, Martiny, Mounport & N'Diaye, 1991



**Fig. 62.** A–H. *Peltamigratus (Peltamigratus) christiei* (Golden & Taylor). A. Posterior end of female showing phasmids. B. Cross-section at vulva. C and D. Tail ends males, lateral and ventral view, respectively. E. *En face* view of female. F. Oesophageal region of female. G. Tail end of female. H. Head end of female. I–Q. *Peltamigratus (Nectopelta) perscitus* (Doucet). I. Head end of female. J. *En face* view of female. K. Cross-section at basal plate of head. L and M. Tail ends of females. N. Lateral field at phasmid. O and P. Tail ends of males, lateral and ventral view, respectively. Q. Female. (A–H. After Sher (1964). I–Q. After Doucet (1980), courtesy *Nematologica*.)

#### Present status

*Peltamigratus (Peltamigratus) christiei* (Golden & Taylor, 1956) Sher, 1964

#### Other species

*Peltamigratus (Peltamigratus) amazonensis* Bittencourt & Huang, 1986

syn. *Aorolaimus amazonensis* (Bittencourt & Huang) Baujard, Castillo, Doucet, Martiny, Mounport & N'Diaye, 1991

- Aorolaimus amazonensis* (Bittencourt & Huang) Ebsary, 1991
- P. (P.) banoae* Rashid, Geraert & Sharma, 1987  
 syn. *Peltamigratus banoae* Rashid, Geraert & Sharma, 1987  
*Aorolaimus banoae* (Rashid, Geraert & Sharma) Baujard, Castillo, Doucet, Martiny, Mounport & N'Diaye, 1991  
*Aorolaimus banoae* (Rashid, Geraert & Sharma) Ebsary, 1991
- P. (P.) browni* Khan & Zakiuddin, 1968  
 syn. *Peltamigratus browni* Khan & Zakiuddin, 1968  
*Aorolaimus browni* (Khan & Zakiuddin) Fortuner, 1987
- P. (P.) cerradoensis* Bittencourt & Huang, 1986  
 syn. *Peltamigratus cerradoensis* Bittencourt & Huang, 1986  
*Aorolaimus cerradoensis* (Bittencourt & Huang) Baujard, Castillo, Doucet, Martiny, Mounport & N'Diaye, 1991  
*Aorolaimus cerradoensis* (Bittencourt & Huang) Ebsary, 1991
- P. (P.) holdemani* Sher, 1964  
 syn. *Peltamigratus holdemani* Sher, 1964  
*Aorolaimus holdemani* (Sher) Fortuner, 1987
- P. (P.) ibiboca* Monteiro & Choudhury, 1978  
 syn. *Peltamigratus ibiboca* Monteiro & Choudhury, 1978  
*Aorolaimus ibiboca* (Monteiro & Choudhury) Fortuner, 1987
- P. (P.) indicus* F.A. Khan, 1972  
 syn. *Peltamigratus indicus* F.A. Khan, 1972  
*Peltamigratus indicus* F.A. Khan & Husain, 1973  
*Aorolaimus indicus* (F.A. Khan) Fortuner, 1987
- P. (P.) levicaudatus* Bittencourt & Huang, 1986  
 syn. *Peltamigratus levicaudatus* Bittencourt & Huang, 1986  
*Aorolaimus levicaudatus* (Bittencourt & Huang) Baujard, Castillo, Doucet, Martiny, Mounport & N'Diaye, 1991  
*Aorolaimus levicaudatus* (Bittencourt & Huang) Ebsary, 1991
- P. (P.) luci* Sher, 1964  
 syn. *Peltamigratus luci* Sher, 1964  
*Aorolaimus luci* (Sher) Fortuner, 1987
- P. (P.) macbethi* Sher, 1964  
 syn. *Peltamigratus macbethi* Sher, 1964  
*Aorolaimus macbethi* (Sher) Fortuner, 1987
- P. (P.) nigeriensis* Sher, 1964  
 syn. *Peltamigratus nigeriensis* Sher, 1964  
*Aorolaimus nigeriensis* (Sher) Fortuner, 1987
- P. (P.) pachyurus* Loof, 1964  
 syn. *Peltamigratus pachyurus* Loof, 1964  
*Aorolaimus pachyurus* (Loof) Fortuner, 1987  
*Peltamigratus thornei* Knobloch, 1969  
*Aorolaimus thornei* (Knobloch) Fortuner, 1987
- P. (P.) paraensis* Bittencourt & Huang, 1986  
 syn. *Peltamigratus paraensis* Bittencourt & Huang, 1986  
*Aorolaimus paraensis* (Bittencourt & Huang) Baujard, Castillo, Doucet, Martiny, Mounport & N'Diaye, 1991  
*Aorolaimus paraensis* (Bittencourt & Huang) Ebsary, 1991

- P. (P.) raskii* Bittencourt & Huang, 1986  
 syn. *Peltamigratus raskii* Bittencourt & Huang, 1986  
*Aorolaimus raskii* (Bittencourt & Huang) Baujard, Castillo, Doucet, Martiny,  
 Mounport & N'Diaye, 1991  
*Aorolaimus raskii* (Bittencourt & Huang) Ebsary, 1991
- P. (P.) regularis* Siddiqi, 1985  
 syn. *Peltamigratus regularis* Siddiqi, 1985  
*Aorolaimus regularis* (Siddiqi) Ebsary, 1991  
*Aorolaimus regularis* (Siddiqi) Baujard, Castillo, Doucet, Martiny &  
 Mounport, 1994
- P. (P.) sheri* Andrásy, 1968  
 syn. *Peltamigratus sheri* Andrásy, 1968  
*Aorolaimus sheri* (Andrásy) Fortuner, 1987
- P. (P.) striatus* Smit, 1971  
 syn. *Peltamigratus striatus* Smit, 1971  
*Aorolaimus striatus* (Smit) Fortuner, 1987
- P. (P.) vigiae* Rashid, Geraert & Sharma, 1987  
 syn. *Peltamigratus vigiae* Rashid, Geraert & Sharma, 1987  
*Aorolaimus vigiae* (Rashid, Geraert & Sharma) Baujard, Castillo, Doucet,  
 Martiny, Mounport & N'Diaye, 1991  
*Aorolaimus vigiae* (Rashid, Geraert & Sharma) Ebsary, 1991

### **Subgenus *Nectopelta* Siddiqi, 1986**

(Figs 59, C; 62, I–Q)

#### **Diagnosis**

Genus *Peltamigratus*. With the characters of the genus *Peltamigratus*. Body 0.7–1 mm long. **Lateral fields in tail region with four incisures, areolated in phasmid region. Cephalic region distinctly annulated, marked by longitudinal grooves or striae;** labial disc distinct. Stylet well developed, about 28–35 µm long; knobs rounded. Male tail enveloped by a large bursa, indented terminally in type species. **Restricted in distribution to South America.**

#### **Type species**

*Nectopelta annulata* (Mulk & Siddiqi, 1982) Siddiqi, 1986

#### **Present status**

*Peltamigratus (Nectopelta) annulatus* Mulk & Siddiqi, 1982  
 syn. *Peltamigratus annulatus* Mulk & Siddiqi, 1982  
*Aorolaimus annulatus* (Mulk & Siddiqi) Fortuner, 1987

#### **Other species**

*Peltamigratus (Nectopelta) areolatus* Bittencourt & Huang, 1986  
 syn. *Peltamigratus areolatus* Bittencourt & Huang, 1986  
*Aorolaimus areolatus* (Bittencourt & Huang) Baujard, Castillo, Doucet,  
 Martiny, Mounport & N'Diaye, 1991  
*Aorolaimus areolatus* (Bittencourt & Huang) Ebsary, 1991  
*Nectopelta areolatus* (Bittencourt & Huang) comb. n.



- P. (N.) longistylus* Doucet, 1980  
 syn. *Peltamigratus longistylus* Doucet, 1980  
*Nectopelta longistylus* (Doucet) Siddiqi, 1986  
*Aorolaimus longistylus* (Doucet) Fortuner, 1987  
*Peltamigratus brevicaudatus* Doucet, 1984  
*Nectopelta brevicaudata* (Doucet) Siddiqi, 1986  
*Aorolaimus brevicaudatus* (Doucet) Fortuner, 1987  
*Peltamigratus conicori* Doucet, 1984  
*Nectopelta conicori* (Doucet) Siddiqi, 1986  
*Aorolaimus conicori* (Doucet) Fortuner, 1987  
*Peltamigratus triticeus* Doucet, 1984  
*Nectopelta triticea* (Doucet) Siddiqi, 1986  
*Aorolaimus triticeus* (Doucet) Fortuner, 1987
- P. (N.) perscitus* Doucet, 1980  
 syn. *Peltamigratus perscitus* Doucet, 1980  
*Nectopelta perscita* (Doucet) Siddiqi, 1986  
*Aorolaimus perscitus* (Doucet) Fortuner, 1987

### Relationship

The subgenus *Nectopelta* differs from the subgenus *Peltamigratus* in having a distinctly annulated cephalic region which is marked by longitudinal grooves, and lateral fields areolated at the phasmids. Some species of *Peltamigratus* (e.g. *P. striatus*) have a striated cephalic region, but they lack distinct longitudinal grooves that divide the cephalic region into six lobes and the characteristic areolation of the lateral fields at the phasmids. *Nectopelta* is restricted to the Neotropical region.

ETYMOLOGY. From Latin *necto* = weave (for areolation), *pelta* = shield, for phasmid; feminine in gender.

The type species was collected around plant roots in Chile. *Peltamigratus* (*Nectopelta*) *conicori*, *P. (N.) longistylus*, *P. (N.) perscita* and *P. (N.) triticea* were collected in the province of Cordoba, Argentina, around the roots of *Cellis tala*, *Cassia aphylla*, *Paspalum* sp. and *Triticum aestivum*, respectively.

## Subfamily Rotylenchoidinae Whitehead, 1958

### syn. Rotylenchinae Golden, 1971

### Pararotylenchinae Baldwin & Bell, 1981

### Diagnosis

Hoplolaimidae. **Vermiform** (including mature female), small to moderately large (0.37–1.2 mm); strongly curved, often **spirally**, rarely arcuate, when relaxed. Body annulation distinct. Lateral fields generally **not areolated behind oesophagus**. **Cephalic region small, conoid-rounded and offset or continuous with body contour; annulations and longitudinal indentations present or absent**; labial disc flattened. **Orifice of dorsal oesophageal gland usually more than one-fourth stylet length behind stylet base**. Subventral glands longer than or equal to dorsal gland. Amphidelphic, or rarely with posterior branch reduced. **Epiptygma obscure**; vulval

lips not modified. **Phasmids small, with pore-like apertures in or near anal region.** Female tail short, rounded, or dorsally convex-conoid, with or without a ventral or terminal process (mucro). Bursa moderately developed, enclosing tail tip or rarely subterminal, not indented terminally. Spicules rather slender, arcuate, pointed, with terminal flanges. Gubernaculum slender, fixed, or protrusible; hypopygium present or absent.

#### Type genus

*Rotylenchoides* Whitehead, 1958

#### Other genera

*Antarctylus* Sher, 1973

*Helicotylenchus* Steiner, 1945

*Orientylus* Jairajpuri & Siddiqi, 1977

*Rotylenchus* Filipjev, 1936

*Varotylus* Siddiqi, 1986

#### Key to genera of Rotylenchoidinae

1. Oesophageal glands extending over intestine mostly ventrally and ventrolaterally ..... 2  
    Oesophageal glands extending over intestine mostly dorsally and dorsolaterally ..... 3
2. Posterior ovary non-functional or absent ..... *Rotylenchoides*  
    Posterior ovary functional ..... *Helicotylenchus*
3. Posterior ovary non-functional or absent ..... *Orientylus*  
    Posterior ovary functional ..... 4
4. Female tail regularly tapering to a small tip, two to three anal body widths long; subventral oesophageal glands asymmetrical ..... *Antarctylus*  
    Female tail not regularly tapering to a small tip, less than two anal body widths long; subventral oesophageal glands symmetrical ..... 5
5. Orifice of dorsal oesophageal gland about half stylet length behind stylet base; gubernaculum fixed ..... *Varotylus*  
    Orifice of dorsal oesophageal gland less than half stylet length behind stylet base; gubernaculum protrusible ..... *Rotylenchus*

#### Genus *Rotylenchoides* Whitehead, 1958

(Fig. 63, B–G)

#### Diagnosis

Rotylenchoidinae. Small-sized (0.37–0.58 mm), arcuate or curved upon relaxation. Lateral fields non-areolated behind oesophageal region. Phasmids pore-like, in or near anal region. Cephalic region small, low continuous; framework heavily sclerotized; labial disc indistinct. Stylet massive, about three times cephalic region width long. **Orifice of dorsal gland less than half stylet length behind base of stylet.**

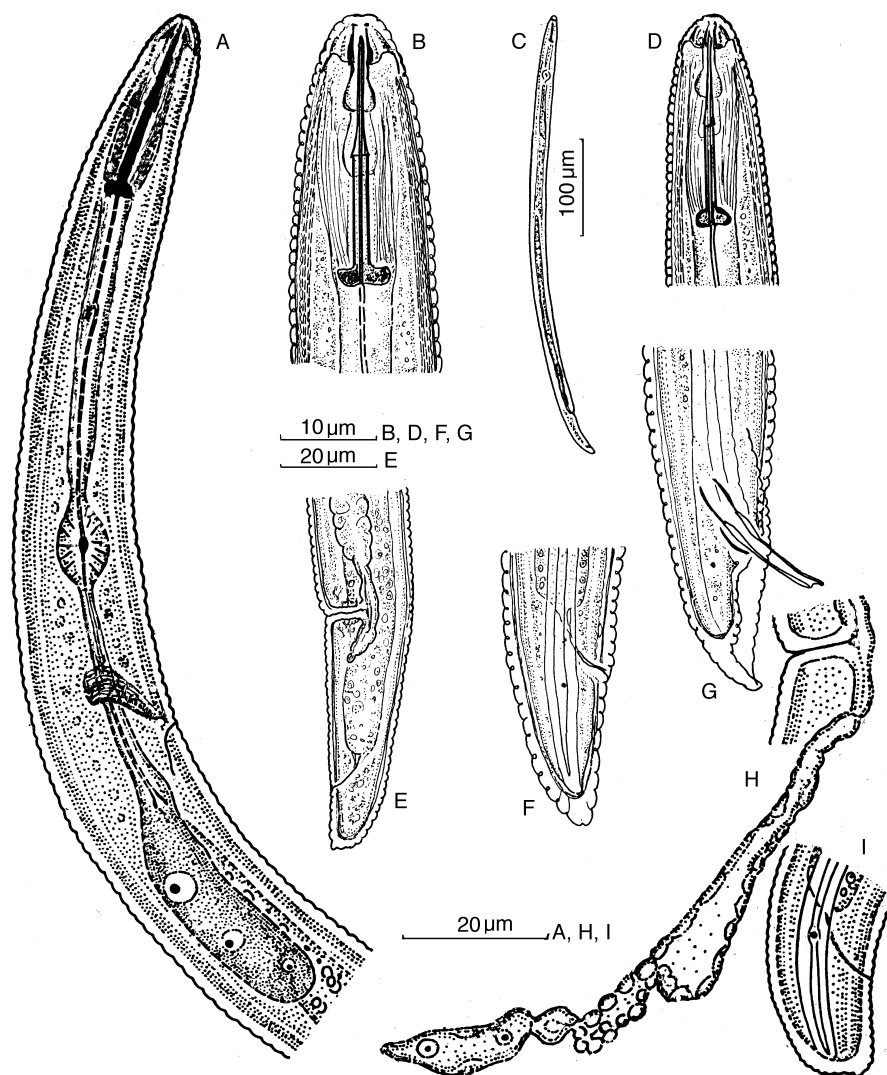


Fig. 63. B-G. *Rotylenchoides subterminalis* Siddiqi. A, H & I. *Orientylus orientalis* (Siddiqi & Husain). A. Oesophageal region of female. B and D. Head end of female and male, respectively. C. Female. E, F and I. Tail ends of females. G. Tail end of male. H. Posterior reproductive branch of female. (A, H and I. After Siddiqi & Husain (1964). B-G. After Siddiqi (1995), courtesy *Afro-Asian Journal of Nematology*.)

Excretory pore behind hemizonid. **Posterior branch of female reproductive organs non-functional, reduced or represented by a uterine sac.** Anterior ovary normal, outstretched, oocytes mostly in a row. Spermatheca round, with minute round sperm in impregnated females. **Vulva posterior, at 74–92% of body length.** Female tail short, hemispherical, dorsally convex-conoid to conoid. Spicules slender distally. Gubernaculum fixed.

### Type species

- Rotylenchoides brevis* Whitehead, 1958  
syn. *Helicotylenchus brevis* (Whitehead) Fortuner, 1984

### Other species

- Rotylenchoides affinis* Luc, 1960  
syn. *Helicotylenchus affinis* (Luc) Fortuner, 1984  
*R. attenuatus* Siddiqi, 1995  
syn. *Helicotylenchus* (*Rotylenchoides*) *attenuatus* Siddiqi, 1995  
*R. cheni* Zhu, Lan, Hu, Yang & Wang, 1991 (? = nomen nudum)  
*R. delanus* (Marais, 1998) comb. n.  
syn. *Helicotylenchus delanus* Marais, 1998  
*R. intermedius* Luc, 1960  
syn. *Helicotylenchus intermedius* (Luc) Siddiqi & Husain, 1964  
*R. neoformis* (Siddiqi & Husain, 1964) Sher, 1966  
syn. *Helicotylenchus neoformis* Siddiqi & Husain, 1964  
*R. subterminalis* Siddiqi, 1995  
syn. *Helicotylenchus* (*Rotylenchoides*) *subterminalis* Siddiqi, 1995  
*R. valdeclarus* Orton Williams, 1983  
syn. *Helicotylenchus valdeclarus* (Orton Williams) Ebsary, 1991  
*R. variocaudatus* Luc, 1960  
syn. *Helicotylenchus variocaudatus* (Luc) Fortuner, 1984  
*R. whiteheadi* Ganguly & Khan, 1987  
syn. *Helicotylenchus whiteheadi* (Ganguly & Khan) Ebsary, 1991  
*Rotylenchus whiteheadi* (Ganguly & Khan) Castillo, Vovlas, Gomez Barcina & Lamberti, 1993

### Remarks

Whitehead (1958) proposed the genus *Rotylenchoides* for *R. brevis*, which was similar to *Helicotylenchus* spp. except for the presence of a postvulval uterine sac in place of a posterior reproductive branch with a functional ovary. Luc (1960) added three species to the genus, including *R. intermedius*, which had a posterior branch of the reproductive organs, although greatly reduced. Siddiqi & Husain (1964) described a similar species as *Helicotylenchus neoformis* and stated that the reduction in size of the posterior branch was not of generic value, but Sher (1966) upheld the generic value of this character and transferred *H. neoformis* to *Rotylenchoides*. It is clear that the posterior shift of the vulva in *Rotylenchoides* results in the regression of the posterior reproductive branch. Fortuner (1984) did not realize the generic importance of this character and synonymized *Rotylenchoides* with *Helicotylenchus*. Siddiqi (1971) redefined *Rotylenchoidinae* Whitehead, 1958 and placed the didelphic genus *Helicotylenchus* along with *Rotylenchoides* in this subfamily. Siddiqi (1995) described two new species of *Rotylenchoides* and recognized its generic rank, suggesting that it could be considered as a subgenus of *Helicotylenchus*.

ETYMOLOGY. From *Rotylenchus*, and Greek *eidos* = shape, likeness.

The type species was collected from roots of *Musa paradisiaca* var. *sapientum* at Mbuzii, Lushoto district, Tanzania. A key to *Rotylenchoides* spp. was given by Orton Williams (1983).

### Genus *Helicotylenchus* Steiner, 1945

syn. *Zimmermannia* Shamsi, 1973

(Fig. 64)

#### Diagnosis

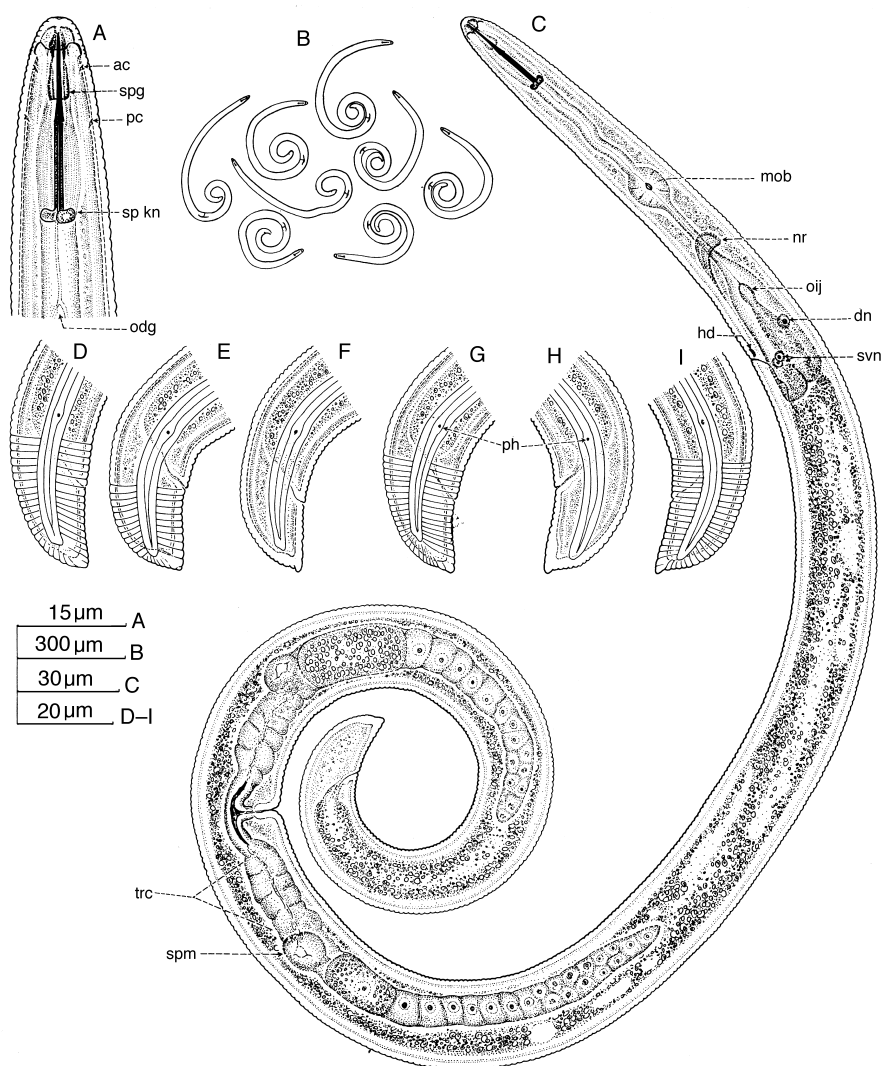
Rotylenchoidinae. Small to medium-sized (0.4–1.2 mm). Females spirally coiled or rarely arcuate. Cephalic region low or elevated, continuous or rarely offset, with or without annulation; **no longitudinal indentations on annules**. Stylet robust, about three to four times maximum width of cephalic region. Orifice of dorsal oesophageal gland one-fourth to a little more than half of stylet length behind base of stylet. Postcorporate bulb well developed, usually slightly offset from precorpus (stylet and bulb slightly reduced in males of some species). Excretory pore behind hemizonid, near base of isthmus. **Oesophageal glands forming a wraparound over anterior end of intestine, longest overlap being ventral**. Oesophago-intestinal junction with a small cuticular valvula. Intestine rarely with fasciculi; not overlapping rectum. **Both branches of female reproductive organs well developed and functional**. Female tail short, hemispherical, dorsally convex-conoid, with or without a ventral or terminal projection. Male tail short (less than two anal body widths), conical, with a distinct terminal hyaline portion. Bursa enveloping entire tail tip, rarely subterminal. Gubernaculum trough- or rod-shaped, fixed; telamon not seen.

#### Type species

*Helicotylenchus nannus* Steiner, 1945

#### Present status

*Helicotylenchus dihystra* (Cobb, 1893) Sher, 1961  
 syn. *Tylenchus dihystra* Cobb, 1893  
*Tylenchus olaae* Cobb, 1906  
*Tylenchorhynchus olaae* (Cobb) Micoletzky, 1922  
*Helicotylenchus olaae* (Cobb) Siddiqi, 1986  
*Aphelenchus dubius* var. *peruensis* Steiner, 1920  
*Tylenchus spiralis* Cassidy, 1930  
*Helicotylenchus spiralis* (Cassidy) Sher, 1961  
*Helicotylenchus spiralis* (Cassidy) Siddiqi, 1986  
*Helicotylenchus nannus* Steiner, 1945  
*Helicotylenchus crenatus* Das, 1960  
*Helicotylenchus flatus* Román, 1965  
*Helicotylenchus punicae* Swarup & Sethi, 1968  
*Helicotylenchus paraconcaus* Rashid & Khan, 1974  
*Helicotylenchus reversus* Sultan, 1985  
*Helicotylenchus membranatus* Xie & Feng, 1993



**Fig. 64.** *Helicotylenchus dihystra* (Cobb). A–I. Topotype females. A. Head end. B and C. Females. D–I. Tail ends. Ac, anterior cephalid; dn, dorsal oesophageal gland nucleus; hd, hemizonid; mob, median oesophageal bulb; nr, nerve ring; odg, orifice of dorsal gland nucleus; oij, oesophago-intestinal junction; pc, posterior cephalid; ph, phasmid; spg, stylet guide; spkn, stylet knobs; spm, spermatheca; svn, subventral gland nuclei; trc, tricolomella. (After Siddiqi, 1972a.)

#### Other species

*Helicotylenchus abuharazi* Zeidan & Geraert, 1990

*H. abunaamai* Siddiqi, 1972

*H. acunae* Fernández, Razjivin, Ortega & Quincosa, 1980

*H. acutucaudatus* Fernandez, Razjivin, Ortega & Quincosa, 1980

- H. acutus* Teben'kova, 1983  
*H. aerolatus* Van den Berg & Heyns, 1975  
*H. africanus* (Micoletzky, 1916) Andrásy, 1958  
    syn. *Tylenchus robustus* var. *africanus* Micoletzky, 1916  
        *Tylenchorhynchus africanus* (Micoletzky) Micoletzky, 1922  
        *Rotylenchus africanus* (Micoletzky) Filipjev, 1936  
*H. agricola* Elmiligy, 1970  
*H. alinae* Khan, Singh & Lal, 1998  
*H. amabilis* Volkova, 1987  
*H. amplius* Anderson & Eveleigh, 1982  
*H. angularis* Mulk & Siddiqi, 1982  
*H. anhelicus* Sher, 1966  
*H. annobonensis* (Gadea, 1960) Siddiqi, 1972  
    syn. *Tylenchorhynchus africanus* var. *annobonensis* Gadea, 1960  
*H. apiculus* Román, 1965  
*H. aquali* Khan & Nanjappa, 1972  
    syn. *Helicotylenchus arachisi* Mulk & Jairajpuri, 1975 (syn. by Lal & Khan, 1997)  
        *Helicotylenchus bihari* Mulk & Jairajpuri, 1975 (syn. by Lal & Khan, 1997)  
        *Helicotylenchus wajih* Sultan, 1981 (syn. by Lal & Khan, 1997)  
*H. arliani* Khan, Singh & Lal, 1998  
*H. astriatus* Khan & Nanjappa, 1972  
*H. atlanticus* Fernández, Razjivin, Ortega & Quincosa, 1980  
*H. australis* Siddiqi, 1972  
*H. babikeri* Zeidan & Geraert, 1990  
*H. bambesae* Elmiligy, 1970  
*H. belli* Sher, 1966 (perhaps a synonym of *H. oryzae*)  
*H. bifurcatus* Fernández, Razjivin, Ortega & Quincosa, 1980  
*H. borinquensis* Román, 1965 (sp. inq. for Fortuner *et al.*, 1981)  
*H. caipora* Monteiro & Medonça, 1972  
*H. californicus* Sher, 1966  
*H. canadensis* Waseem, 1961  
    syn. *Helicotylenchus cairnsi* Waseem, 1961  
*H. canalis* Sher, 1966  
*H. caribensis* Román, 1965 (sp. inq. for Fortuner *et al.*, 1981)  
*H. carolinensis* Sher, 1966  
*H. caudatus* Sultan, 1985  
*H. cavenessi* Sher, 1966  
*H. cedreus* Volkova, 1987  
*H. cephalatus* Brzeski, 1998 (? syn. of *H. spitsbergensis*)  
*H. certus* Eroshenko & Nguen Vu Thanh, 1981  
*H. clarkei* Sher, 1966  
*H. coffae* Eroshenko & Nguen Vu Thanh, 1981  
*H. concavus* Roman, 1961  
*H. conicephalus* Siddiqi, 1972  
*H. conicus* Baydulova 1981  
*H. coomansi* Ali & Loof, 1975  
*H. cornurus* Anderson, 1974

- H. craigi* Knobloch & Laughlin, 1973  
*H. crassatus* Anderson, 1973  
*H. crenacauda* Sher, 1966  
     syn. *Helicotylenchus pteracercus* Singh, 1971  
         *Helicotylenchus indenticaudatus* Mulk & Jairajpuri, 1975  
         *Helicotylenchus paracrenacauda* Phukan & Sanwal, 1981  
         *Helicotylenchus pteracercusoides* Fotedar & Kaul, 1985  
         *Helicotylenchus indentatus* Chaturvedi & Khera, 1979  
*H. curvatus* Román, 1965  
*H. curvicaudatus* Fernández, Razjivin, Ortega & Quincosa, 1980  
*H. delhiensis* Khan & Nanjappa, 1972  
*H. densibullatus* Siddiqi, 1972  
*H. depressus* Yeates, 1967  
*H. digitatus* Siddiqi & Husain, 1964  
*H. digitiformis* Ivanova, 1967  
*H. dignus* Eroshenko & Nguen Vu Thanh, 1981  
*H. digonicus* Perry, in Perry, Darling & Thorne, 1959  
     syn. *Helicotylenchus broadbalkiensis* Yuen, 1964  
*H. dihystreroide*s Siddiqi, 1972  
*H. discocephalus* Firoza & Maqbool, 1993  
*H. distinctus* Mohilal, Anandi & Dhanachand, 1998  
*H. dolichodoryphorus* Sher, 1966  
*H. dumicola* Siddiqi, 1995  
*H. egyptiensis* Tarjan, 1964  
*H. elegans* Román, 1965  
*H. eletropicus* Darekar & Khan, 1980  
*H. erythrinae* (Zimmermann, 1904) Golden, 1956  
     syn. *Tylenchus erythrinae* Zimmermann, 1904  
         *Tylenchorhynchus erythrinae* (Zimmermann) Bally & Reydon, 1931  
         *Anguillulina erythrinae* (Zimmermann) Goodey, 1932  
         *Rotylenchus erythrinae* (Zimmermann) Goodey, 1951  
         *Helicotylenchus* (Zimmermannia) *erythrinae* Zimmermann (Shamsi, 1973)  
         *Zimmermannia erythrinae* (Zimmermann) Shamsi, 1973  
         *Rotylenchus melancholicus* Lordello, 1955  
         *Helicotylenchus melancholicus* (Lordello) Andrassy, 1958  
         *Helicotylenchus spicaudatus* Tarjan, 1964  
*H. exallus* Sher, 1966  
     syn. *Helicotylenchus regularis* Phillips, 1971  
*H. falcatus* Eroshenko & Nguen Vu Thanh, 1981  
*H. fericulus* Siddiqi, 1995  
*H. ferus* Eroshenko & Nguen Vu Thanh, 1981  
*H. girus* Saha, Chawla & Khan, 1974  
     syn. *Helicotylenchus incisus* Darekar & Khan, 1979 (syn. by Lal & Khan, 1997)  
         *Helicotylenchus obtusicaudatus* Darekar & Khan, 1979 (syn. by Lal & Khan, 1997)  
*H. glissus* Thorne & Malek, 1968 (syn. of *H. dihystra* for Fortuner *et al.*, 1981)  
*H. goldeni* Sultan & Jairajpuri, 1979



- H. goodi* Tikyani, Khera & Bhatnagar, 1969  
syn. *Helicotylenchus gratus* Patil & Khan, 1983 (syn. by Lal & Khan, 1997)
- H. graminophilus* Fotedar & Mahajan, 1974
- H. haki* Fotedar & Mahajan, 1974
- H. hazratbalensis* Fotedar & Handoo, 1974 (syn. of *H. indicus* for Lal & Khan, 1994)
- H. holguinensis* Sagitov, Sampedro, Santos & Paneke, 1978
- H. hydrophilus* Sher, 1966
- H. impar* Prasad, Khan & Chawla, 1965 (syn. of *H. retusus* for Nandakumar & Khera, 1970)  
syn. *Helicotylenchus paragirus* Saha, Chawla & Khan, 1974 (syn. by Lal & Khan, 1997; syn of *H. retusus* for Orton Williams, 1980)  
*Helicotylenchus steineri* Fotedar & Mahajan, 1974 (syn. by Lal & Khan, 1997)
- H. imperialis* Rashid & Khan, 1974
- H. indicus* Siddiqi, 1963  
syn. *Helicotylenchus plumariae* Khan & Basir, 1964  
*Helicotylenchus persici* Saxena, Chhabra & Joshi, 1973
- H. inifatis* Fernández, Razjivin, Ortega & Quincosa, 1980
- H. interrogativus* Eroshenko, 1981
- H. insignis* Khan & Basir, 1964 (valid species for Fotedar & Kaul, 1986)  
syn. *Helicotylenchus teres* Gaur & Prasad, 1974  
*Helicotylenchus thornei* Gupta & Chhabra, 1967, nec *H. thornei* Román, 1965  
*Helicotylenchus bakeri* Gupta & Chhabra, 1975 (nom. nov. for *H. thornei* Gupta & Chhabra)
- H. issykkulensis* Sultanalieva, 1983
- H. jammuensis* Fotedar & Mahajan, 1974
- H. jojutlensis* Zavaleta-Majia & Sosa Moss, 1979
- H. kashmirensis* Fotedar & Heyns, 1974 (syn. of *H. retusus* for Lal & Khan, 1997)
- H. kermarreci* Marais, Van den Berg, Quénéhervé & Tiedt, 1999
- H. kherai* Kumar, 1982
- H. labiatus* Román, 1965
- H. labiodiscinus* Sher, 1966
- H. laevicaudatus* Eroshenko & Nguen Vu Thanh, 1981
- H. leiocephalus* Sher, 1966
- H. lemoni* Firoza & Maqbool, 1996
- H. limarius* Eroshenko, Tyau, Tkhan & Kan, 1985
- H. limatus* Siddiqi, 1995
- H. lissocaudatus* Fernández, Razjivin, Ortega & Quincosa, 1980
- H. lobus* Sher, 1966
- H. longicaudatus* Sher, 1966
- H. macronatus* Mulk & Jairajpuri, 1975 (syn. of *H. indicus* for Lal & Khan, 1994)
- H. martini* Sher, 1966  
syn. *Helicotylenchus krugeri* Van den Berg & Heyns, 1975
- H. macrostylus* Marais & Quénéhervé, 1996
- H. microcephalus* Sher, 1966  
syn. *Helicotylenchus mangiferensis* Elmiligy, 1970  
*Helicotylenchus magnicephalus* Phukan & Sanwal, 1981

- Helicotylenchus belurensis* Singh & Khera, 1980
- H. microdorus* Prasad, Khan & Chawla, 1965  
(probable synonym of *H. indicus* for Nandakumar & Khera, 1970)
- H. microlobus* Perry in Perry, Darling & Thorne, 1959  
syn. *Helicotylenchus bradys* Thorne & Malek, 1968
- H. microtylus* Firoza & Maqbool, 1993
- H. minutus* Van den Berg & Cadet, 1991
- H. minzi* Sher, 1966
- H. monstruosus* Eroshenko, 1984
- H. montanus* Teben'kova, 1983
- H. morasii* Darekar & Khan, 1980
- H. mucrogaleatus* Fernández, Razjivin, Ortega & Quincosa, 1980
- H. mucronatus* Siddiqi, 1964
- H. multicinctus* (Cobb, 1893) Golden, 1956  
syn. *Tylenchus multicinctus* Cobb, 1893  
*Tylenchorhynchus multicinctus* (Cobb) Micoletzky, 1922  
*Anguillulina multicincta* (Cobb) Goodey, 1932  
*Rotylenchus multicinctus* (Cobb) Filipjev, 1936  
*Rotylenchus iperoiguensis* Carvalho, 1956  
*Helicotylenchus iperoiguensis* (Carvalho) Andrassy, 1958  
*Orientylus karachiensis* Maqbool & Ghazala, 1984  
*Rotylenchus karachiensis* (Maqbool & Ghazala) Fortuner, 1987  
*Helicotylenchus karachiensis* (Maqbool & Ghazala) comb. n.
- H. mundus* Siddiqi, 1995
- H. neopaxilli* Inserra, Vovlas & Golden, 1979
- H. nigeriensis* Sher, 1966
- H. nitens* Siddiqi, 1995
- H. notabilis* Eroshenko & Nguen Vu Thanh, 1981
- H. obliquus* Maqbool & Shahina, 1986
- H. oleae* Inserra, Vovlas & Golden, 1979
- H. orientalis* Sagitov, Sanpedro, Santos & Paneke, 1978  
syn. *Helicotylenchus sagitovi* Fortuner, Merny & Roux, 1981( = invalidated replacement name)
- H. orthosomaticus* Siddiqi, 1972
- H. oryzae* Fernández, Razjivin, Ortega & Quincosa, 1980
- H. oscephalus* Anderson, 1979 (syn. of *H. teleductus* for Fotedar & Kaul, 1986)
- H. parabelli* Volkova, 1987
- H. paracanalisis* Sauer & Winoto, 1975  
syn. *Helicotylenchus trivandranus* Mohandas, 1976
- H. paradihysteroides* Darekar & Khan, 1979
- H. paraplasyurus* Siddiqi, 1972
- H. parapteracercus* Sultan, 1981
- H. pasohi* Sauer & Winoto, 1975
- H. paxilli* Yuen, 1964
- H. pisi* Swarup & Sethi, 1968
- H. planquettii* Marais & Quénéhervé, 1999
- H. platyurus* Perry in Perry, Darling & Thorne, 1959

- H. pricei* Siddiqi, 1995  
*H. pseudodigonicus* Szczygieł, 1970  
*H. pseudopaxilli* Fernández, Razjivin, Ortega & Quincosa, 1980  
*H. pseudorobustus* (Steiner, 1914) Golden, 1956  
syn. *Tylenchus robustus* var. *pseudorobustus* Steiner, 1914  
*Helicotylenchus phalerus* Anderson, 1974  
*H. raskii* Narayanaswamy, 1987  
*H. retusus* Siddiqi & Brown, 1964  
syn. *Helicotylenchus valecus* Sultan, 1981 (syn. for Lal & Khan, 1997)  
*H. reynosus* Razjivin, O'Relly & Milian, 1973  
*H. rohtangus* Jairajpuri & Baqri, 1973 (syn. of *H. retusus* for Lal & Khan, 1997)  
*H. rotundicauda* Sher, 1966 (syn. of *H. dihystra* for Fortuner *et al.*, 1981)  
*H. sacchari* Razjivin, O'Relly & Milian, 1973  
*H. saccharumi* Jain, Upadhyay & Singh, 1989  
*H. sandersae* Ali & Loof, 1975  
*H. saxeus* Siddiqi, 1995  
*H. scoticus* Boag & Jairajpuri, 1985  
*H. serenus* Siddiqi, 1963  
*H. seshadrii* Singh & Khera, 1980  
*H. shakili* Sultan, 1981  
*H. sharafati* Mulk & Jairajpuri, 1975  
*H. sheri* Jain, Upadhyay & Singh, 1989  
*H. sieversii* Razjivin, 1971  
*H. silvaticus* Lal & Khan, 1990  
*H. similis* Fernández, Razjivin, Ortega & Quincosa, 1980  
*H. solani* Rashid & Khan, 1971  
*H. sparsus* Fernández, Razjivin, Ortega & Quincosa, 1980  
*H. spitsbergensis* Loof, 1971  
*H. striatus* Firoza & Maqbool, 1994  
*H. stylocercus* Siddiqi & Pinochet, 1979  
*H. subtropicalis* Fernández, Razjivin, Ortega & Quincosa, 1980  
*H. talonus* Siddiqi, 1972 (syn. of *H. bambesae* for Ali & Geraert, 1975)  
*H. tangericus* Sultan, 1981 (syn. of *H. retusus* for Lal & Khan, 1997)  
*H. teleductus* Anderson, 1974 (syn. of *H. dihystra* for Fortuner *et al.*, 1981)  
*H. thornei* Roman, 1965  
*H. trapezoidicaudatus* Fotedar & Kaul, 1985  
*H. tropicus* Roman, 1965  
*H. truncatus* Roman, 1965  
*H. tumidicaudatus* Phillips, 1971  
*H. tunisiensis* Siddiqi, 1964  
*H. unicus* Fernandez, Razjivin, Ortega & Quincosa, 1980  
*H. urobelus* Anderson, 1978  
*H. ussuriensis* Eroshenko, 1981  
*H. variabilis* Phillips, 1971  
*H. varicaudatus* Yuen, 1964  
*H. ventroprojectus* Patil & Khan, 1983  
*H. verecundus* Zarina & Maqbool, 1991

- H. verrucosus* Fernandez, Razjivin, Ortega & Quincosa, 1980  
*H. vietnamensis* Eroshenko, Tyau, Tkhan & Kan, 1985  
*H. vindex* Siddiqi, 1995  
*H. vulgaris* Yuen, 1964  
*H. willmottae* Siddiqi, 1972 (syn. of *H. retusus* for Lal & Khan, 1997)

### Species inquirendae

- Helicotylenchus brassicae* Rashid, 1972  
*H. hoplocauda* Manjrekar, 1972 (close to *H. impar*, *H. girus*, *H. paragirus*, *H. incisus* and *H. obtusicaudatus*, which are all from India and difficult to differentiate from each other).  
*H. leucernis* Khan & Ahmad, 1970

### Note

*Zimmermannia* was proposed by Shamsi (1973) as a subgenus of *Helicotylenchus* for *H. erythrinae* as type and only species in the subgenus, on the character of the presence of a mucro on the tail tip which, in the male, is not enclosed by the bursa.

ETYMOLOGY. From Greek *helix* = a coil (for body posture when relaxed), and *Tylenchus*.

The type species (*H. nannus*) was collected from soil around roots of *Phaseolus lunatus* L. (lima bean) at Beltsville, Maryland, USA. Keys to *Helicotylenchus* spp. are given by Fortuner & Wong (1984), Fotedar and Kaul (1986) and Firoza and Maqbool (1994).

### Genus *Varotylus* Siddiqi, 1986

(Fig. 66, F–H)

### Diagnosis

Rotylenchoidinae. Small to medium-sized (0.5–1 mm), spiral upon relaxation. Phasmids preanal or near to anus. Lateral fields with four incisures, not areolated. Cephalic region small, continuous, indistinctly or not annulated; longitudinal indentations on annules absent. Stylet well developed. **Orifice of dorsal oesophageal gland about half stylet length behind stylet base.** Median bulb with large refractive thickenings. Oesophageal glands elongate, extending over dorsal, dorsolateral and lateral sides of intestine; **subventral glands lying in a subdorsal to lateral position**, extending past the dorsal gland. Oesophago-intestinal junction indistinct, anterior to glands. **Didelphic; both ovaries well developed. Female tail dorsally convex-conoid to rounded**, with or without a ventral projection, less than 1.5 anal body widths long. Juvenile tail narrower terminally than that of female. Male, where known, with bursa enveloping tail; spicules tylenchoid and **gubernaculum fixed, lacking titillae and telamon.**

### Type species

- Varotylus varus* (Jairajpuri & Siddiqi, 1979) Siddiqi, 1986  
 syn. *Orientylus varus* Jairajpuri & Siddiqi, 1979  
*Rotylenchus varus* (Jairajpuri & Siddiqi) Zancada & Lima, 1986

## Other species

- Varotylus basiri* (Khan & Khan, 1982) Siddiqi, 1986  
 syn. *Orientylus basiri* Khan & Khan, 1982  
*Rotylenchus basiri* (Khan & Khan) Fortuner, 1987
- V. citri* (Rashid & Khan, 1976) Siddiqi, 1986  
 syn. *Rotylenchus citri* Rashid & Khan, 1976  
*Orientylus citri* (Rashid & Khan) Jairajpuri & Siddiqi, 1979
- V. elegans* (Khan & Khan, 1982) Siddiqi, 1986  
 syn. *Orientylus elegans* Khan & Khan, 1982  
*Rotylenchus elegans* (Khan & Khan) Fortuner, 1987
- V. helicus* (Husain & Khan, 1969) Siddiqi, 1986  
 syn. *Rotylenchus helicus* Husain & Khan, 1969  
*Orientylus helicus* (Husain & Khan) Jairajpuri & Siddiqi, 1979
- V. himprus* (Sultan, 1980) Siddiqi, 1986  
 syn. *Orientylus himprus* Sultan, 1980  
*Rotylenchus himprus* (Sultan) Fortuner, 1987
- V. peculiaris* (Khan & Khan, 1982) Siddiqi, 1986  
 syn. *Orientylus peculiaris* Khan & Khan, 1982  
*Rotylenchus peculiaris* (Khan & Khan) Fortuner, 1987
- V. ranapoi* (Darekar & Khan, 1982) Siddiqi, 1986  
 syn. *Rotylenchus ranapoi* Darekar & Khan, 1982
- V. secundus* (Mulk & Jairajpuri, 1976) Siddiqi, 1986  
 syn. *Rotylenchus secundus* Mulk & Jairajpuri, 1976  
*Orientylus secundus* (Mulk & Jairajpuri) Jairajpuri & Siddiqi, 1979
- V. siddiqii* (Mulk & Jairajpuri, 1976) Siddiqi, 1986  
 syn. *Rotylenchus siddiqii* Mulk & Jairajpuri, 1976  
*Orientylus siddiqii* (Mulk & Jairajpuri) Jairajpuri & Siddiqi, 1979
- V. symmetricus* (Sultan, 1980) Siddiqi, 1986  
 syn. *Orientylus symmetricus* Sultan, 1980  
*Rotylenchus symmetricus* (Sultan) Fortuner, 1987

ETYMOLOGY. *Varo* from type species name *varus*, and Greek *tylos* = knob.

The type species was found around roots of Napier grass (*Pennisetum purpureum*) in Malawi. Other species were reported from India.

**Genus *Rotylenchus* Filipjev, 1936**

syn. *Anguillulina* (*Rotylenchus* Filipjev, 1936)

***Gottholdsteineria* Andr ssy, 1958**

***Calvatylus* Jairajpuri & Siddiqi, 1977**

***Pararotylenchus* Baldwin & Bell, 1981**

***Interrotylenchus* Eroshenko, 1984**

***Scutellonemoides* Eroshenko, 1984**

***Plesiorotylenchus* Vovlas, Castillo & Lamberti, 1993**

## Diagnosis

*Rotylenchoidinae*. Cephalic region rounded, offset, annulated, or smooth, with or without longitudinal indentations; first annule divided into six sectors (except

*Plesiorotylenchus*); labial disc usually distinct. **Orifice of dorsal oesophageal gland less than one-fourth stylet length behind stylet base.** Oesophageal glands extending over intestine mostly dorsally, or subdorsally to laterally, or forming a pseudobulb abutting intestine. **Didelphic**; ovaries symmetrical. Female tail short, rounded, annulation following its contour. **Phasmids small with pore-like apertures** located at same level in posterior region of body, usually in or near anal region. Spicules robust, distally flanged. Gubernaculum with titillae and telamon in type species. Bursa enclosing tail, not indented terminally.

#### Type subgenus

*Rotylenchus* Filipjev, 1936

#### Other subgenera

*Calvatylus* Jairajpuri & Siddiqi, 1977, grad. n.

*Pararotylenchus* Baldwin & Bell, 1981, grad. n.

*Plesiorotylenchus* Vovlas, Castillo & Lamberti, 1993, grad. n.

#### Key to subgenera of *Rotylenchus*

1. Cephalic region with transverse striae ..... 2  
    Cephalic region without transverse striae ..... 3
2. Oesophageal glands abutting intestine ..... *Pararotylenchus*  
    Oesophageal glands overlapping intestine ..... *Rotylenchus*
3. Cephalic region with numerous longitudinal striae ..... *Plesiorotylenchus*  
    Cephalic region without such striae ..... *Calvatylus*

#### Subgenus *Rotylenchus* Filipjev, 1936

(Fig. 65, A–H)

#### Diagnosis

Genus *Rotylenchus*. Cephalic region rounded, offset, annulated; basal annule with longitudinal indentations; labial disc usually distinct. Orifice of dorsal oesophageal gland less than one-fourth stylet length behind stylet base. Oesophageal glands overlapping anterior end of intestine, mostly dorsally. Ovaries symmetrical. Female tail short, rounded, annulation following its contour. Spicules robust, distally flanged. Gubernaculum with titillae and telamon in type species. Bursa not indented terminally.

#### Type species

*Rotylenchus robustus* (de Man, 1876) Filipjev, 1936

#### Present status

*Rotylenchus* (*Rotylenchus*) *robustus* (de Man, 1876) Filipjev, 1936

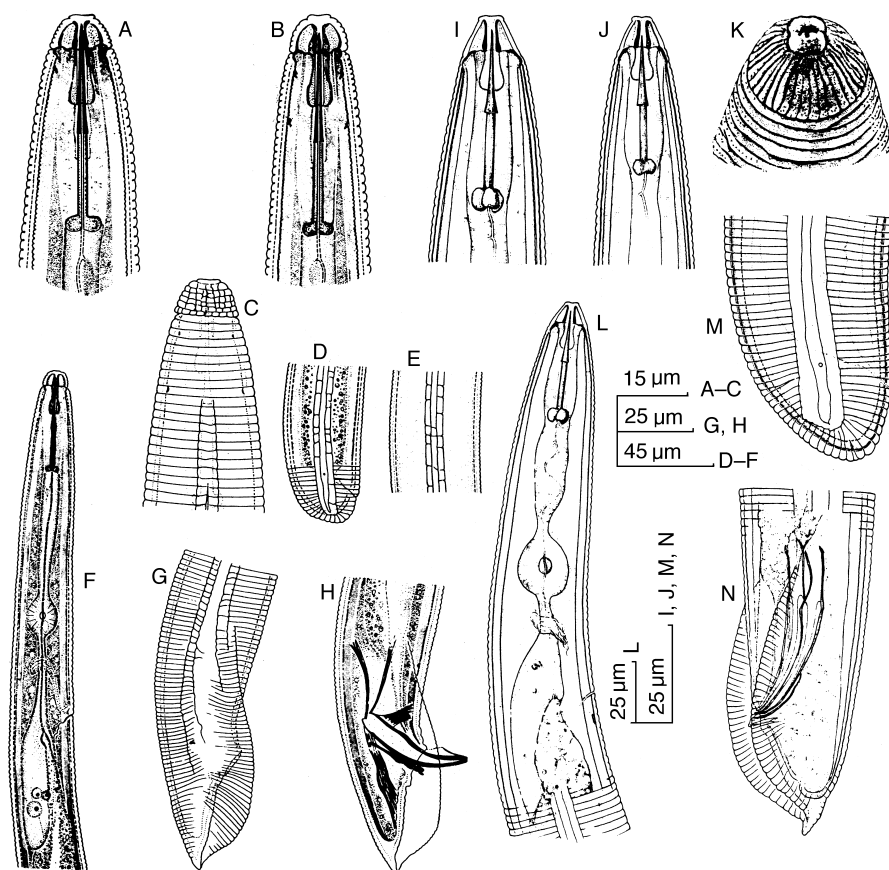
syn. *Tylenchus robustus* de Man, 1876

*Tylenchorhynchus robustus* (de Man) Micoletzky, 1922

*Rotylenchus robustus* (de Man) Filipjev, 1936

*Anguillulina robusta* (de Man) Goodey, 1932

*Hoplolaimus uniformis* Thorne, 1949



**Fig. 65.** A–H. *Rotylenchus robustus* (de Man). I–N. *Plesiorotylenchus striaticeps* Vovlas, Castillo & Lamberti. A, C, I, K. Female head ends. B and J. Male head ends. D and M. Female tail ends. E. Female lateral field at midbody. F and L. Female oesophageal regions. G, H and N. Male tail ends. (A–H. After Siddiqi (1972c). I–N. After Vovlas *et al.* (1993).)

(syn.) *Rotylenchus uniformis* (Thorne) Loof & Oostenbrink, 1958  
*Rotylenchus fallorobustus* Sher, 1965; syn. of *R. robustus* by Seinhorst, 1991  
*Scutellonema picea* Gubina, 1973  
*Rotylenchus picea* (Gubina) Siddiqi, 1986

#### Other species

*Rotylenchus* (*Rotylenchus*) *abnormecaudatus* Van den Berg & Heyns, 1974  
*R. (R.) aceri* Berezina, 1985  
*R. (R.) acuspicaudatus* Van den Berg & Heyns, 1974

- R. (R.) *agnetis* Szczygieł, 1968  
syn. *Interrotylechus agnetis* (Szczygieł) Eroshenko, 1984
- R. (R.) *alii* Maqbool & Shahina, 1986
- R. (R.) *alius* Van den Berg, 1986
- R. (R.) *alpinus* Eroshenko, 1976
- R. (R.) *arsenjevi* (Eroshenko, 1984) Maggenti, Luc, Raski, Fortuner & Geraert, 1988  
syn. *Interrotylechus arsenjevi* Eroshenko, 1984
- R. (R.) *basiri* Geraert & Barooti, 1996
- R. (R.) *bialaebursus* Van den Berg & Heyns, 1974
- R. (R.) *breviglans* Sher, 1965  
syn. *Interrotylechus breviglans* (Sher) Eroshenko, 1984  
*Pararotylechus breviglans* (Sher) Siddiqi, 1986
- R. (R.) *buxophilus* Golden, 1956  
syn. *Gottholdsteineria buxophila* (Golden) Andrassy, 1958  
*Helicotylechus buxophilus* (Golden) Perry in Perry, Darling & Thorne, 1959  
*Rotylechus sheri* Jairajpuri, 1964
- R. (R.) *capensis* Van den Berg & Heyns, 1974
- R. (R.) *capitatus* Eroshenko, 1981  
syn. *Interrotylechus capitatus* (Eroshenko) Eroshenko, 1984
- R. (R.) *capsicumi* Firoza & Maqbool, 1991
- R. (R.) *catharinae* Van den Berg & Heyns, 1974
- R. (R.) *caudaphasmidius* Sher, 1965
- R. (R.) *cazorlaensis* Castillo & Gomez-Barcina, 1988
- R. (R.) *colbrani* Brzeski & Choi, 1998 (was a nom. nov.)  
syn. *Rotylechus brevicaudatus* Colbran, 1962; nec Hopper, 1959; Micoletzky, 1922
- R. (R.) *cypriensis* Antoniou, 1981
- R. (R.) *dalhousiensis* Sultan & Jairajpuri, 1979
- R. (R.) *deckeri* Braasch, 1980 (sp. inq. for Brzeski, 1998)
- R. (R.) *devonensis* Van den Berg, 1976
- R. (R.) *eximius* Siddiqi, 1964
- R. (R.) *fabalus* Baydulova, 1984
- R. (R.) *feroxcis* Eroshenko, 1981  
syn. *Scutellonemoides feroxcis* (Eroshenko) Eroshenko, 1984
- R. (R.) *fragaricus* Maqbool & Shahina, 1986
- R. (R.) *glabratus* Kankina & Teben'kova, 1980
- R. (R.) *goldeni* Firoza & Maqbool, 1993
- R. (R.) *goodeyi* Loof & Oostenbrink, 1958  
syn. *Gottholdsteineria goodeyi* (Loof & Oostenbrink) Andrassy, 1958  
*Helicotylechus goodeyi* (Loof & Oostenbrink) Perry in Perry, Darling & Thorne, 1959
- R. (R.) *gracilidens* (Sauer, 1958) Sauer, 1958  
syn. *Hoplolaimus gracilidens* Sauer, 1958
- R. (R.) *graecus* Vovlas & Troccoli, 1996
- R. (R.) *incultus* Sher, 1965
- R. (R.) *indorobustus* Jairajpuri & Baqri, 1973 (syn. of *R. robustus* for Brzeski, 1998)  
syn. *Scutellonema petersi* Mahajan, 1977  
*R. petersi* (Mahajan) Mattaar & Loof, 1985 (syn. of *R. robustus* for Brzeski, 1998)



- R. (R.) ivanovae* Kankina & Teben'kova, 1980  
*R. (R.) jagatpurensis* Sultan, 1985  
*R. (R.) karoensis* Van den Berg, 1986  
*R. (R.) kenti* Van den Berg, 1989  
*R. (R.) labiodiscus* Wouts & Sturhan, 1999  
*R. (R.) laurentinus* Scognamiglio & Talamé, 1973  
*R. (R.) lobatus* Sultan, 1985  
*R. (R.) mabelei* Van den Berg & De Waele, 1989  
*R. (R.) magnus* Zancada, 1986  
     Subspecies: *R. (R.) magnus magnus* Zancada, 1986  
                   *R. (R.) magnus jaeni* Castillo, Vovlas, Gómez-Barcina & Lamberti, 1994  
*R. (R.) mesorobustus* Zancada, 1986  
*R. (R.) microstriatus* Siddiqi & Corbett, 1982  
*R. (R.) mirus* Van den Berg, 1986  
*R. (R.) neorobustus* Sultan & Jairajpuri, 1979  
*R. (R.) pakistanensis* Maqbool & Shahina, 1986  
*R. (R.) phaliurus* Siddiqi & Pinochet, 1979  
*R. (R.) pruni* Rashid & Husain, 1972  
*R. (R.) pumilus* (Perry in Perry, Darling & Thorne, 1959) Sher, 1961  
     syn. *Helicotylenchus pumilus* Perry in Perry, Darling & Thorne, 1959  
*R. (R.) quartus* (Andrássy, 1958) Sher, 1961  
     syn. *Gottholdsteineria quarta* Andrássy, 1958  
         *Helicotylenchus quartus* (Andrássy) Perry in Perry, Darling & Thorne, 1959  
         *Interrotylenchus quartus* (Andrássy) Eroshenko, 1984  
*R. (R.) rugatocuticulatus* Sher, 1965  
*R. (R.) sabarlyi* Massese & Germani, 1998  
*R. (R.) salinus* Tebenkova, 1982  
*R. (R.) satsilanicus* Sultan, 1985  
*R. (R.) tenericaudatus* Zhao, Liu, Duan, & Liu, 1996  
*R. (R.) triannulatus* Van den Berg & Heyns, 1974  
*R. (R.) troncapitatus* Scotto la Massese & Germani, 1998 (perhaps belongs to *R. (Plesiorotylenchus)*)  
*R. (R.) unisexus* Sher, 1965  
*R. (R.) usitatus* Van den Berg & Heyns, 1974  
*R. (R.) wallacei* Nobbs, 1990

### Species inquirendae

- Tylenchus robustus* var. *exiguus* Kreis, 1924 (junior primary  
     homonym of *Tylenchus exiguus* de Man, 1876  
     = *Tylenchus kreisi* Fortuner, 1985)  
*Rotylenchus steueri* (Stefański, 1916) Siddiqi, 1986 (senior synonym of *R. buxophilus*,?  
     suppressed by ICZN)  
     syn. *Aphelenchus steueri* Stefański, 1916  
         *Helicotylenchus steueri* (Stefański) Sher, 1961

### Nomina nuda

- Rotylenchus julaharensis* Kapoor, 1983  
*Rotylenchus yarikahensis* Kapoor, 1983

ETYMOLOGY. *Ro* from first letters of type species name *robustus*, and *Tylenchus*.

The type species was found in clay soil near Leiden, Holland. Geraert and Barooti (1996) gave a key to species of *Rotylenchus* which showed that several nominal species were difficult to distinguish.

### Subgenus *Calvatylus* Jairajpuri & Siddiqi, 1977

(Fig. 66, A–E)

#### Diagnosis

Genus *Rotylenchus*. **Cephalic region** hemispherical or conoid-truncate, slightly offset, **lacking distinct annulation**; labial disc distinct. Oesophageal glands overlapping intestine dorsally and dorsolaterally. Didelphic; ovaries symmetrical. Female tail dorsally convex-conoid, about one anal body width or less long. Bursa enveloping tail, not indented. **Gubernaculum fixed, lacking titillae. Hypoptygma present on posterior lip of cloaca.**

#### Type species

*Calvatylus calvus* (Sher, 1965) Jairajpuri & Siddiqi, 1977

#### Present status

*Rotylenchus* (*Calvatylus*) *calvus* Sher, 1965  
syn. *Rotylenchus calvus* Sher, 1965

#### Other species

*Rotylenchus* (*Calvatylus*) *heredicus* (Jairajpuri & Siddiqi, 1977) Ferraz, 1980  
syn. *Calvatylus heredicus* Jairajpuri & Siddiqi, 1977  
*Rotylenchus heredicus* (Jairajpuri & Siddiqi) Ferraz, 1980  
*R. (C.) nexus* Ferraz, 1980  
syn. *Rotylenchus nexus* Ferraz, 1980  
*Calvatylus nexus* (Ferraz) Siddiqi, 1986

ETYMOLOGY. *Calva* from the type species name *calvus*, and Greek *tylos* = knot, knob.

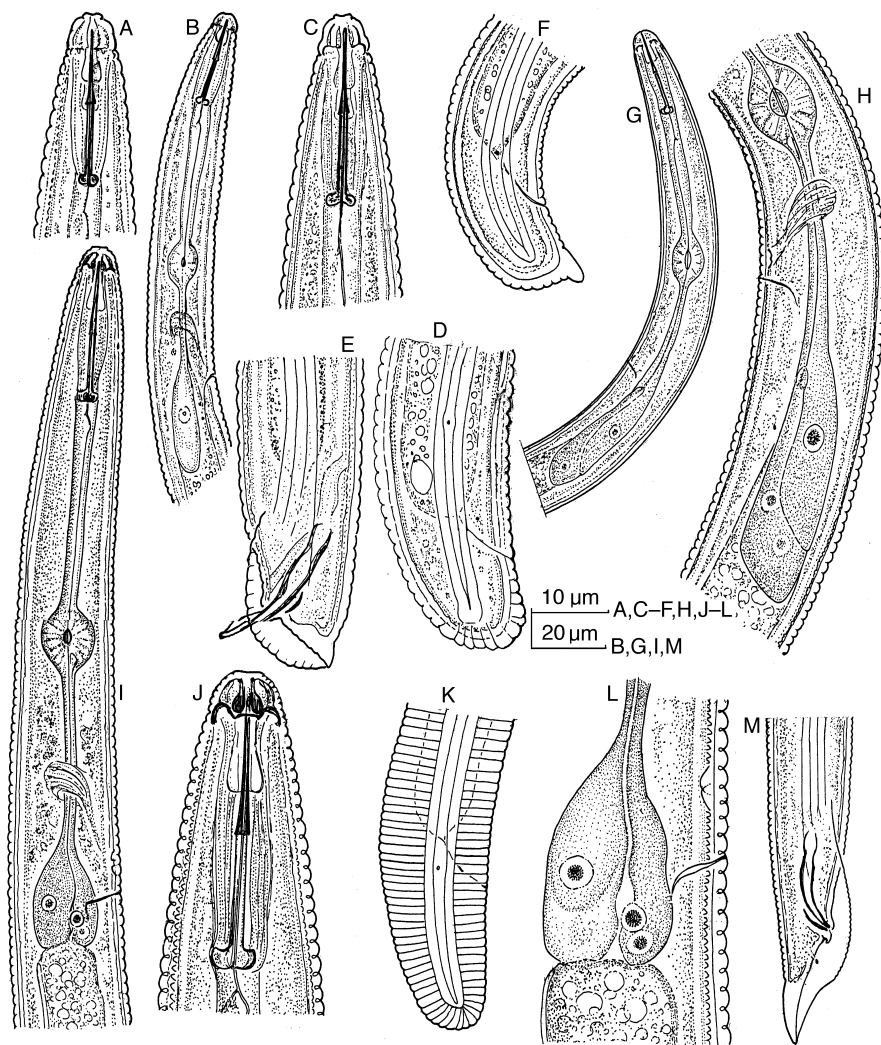
The type species was collected from nursery soil at Santa Ana, El Salvador.

### Subgenus *Pararotylenchus* Baldwin & Bell, 1981, **grad. n.**

(Fig. 66, I–M)

#### Diagnosis

Genus *Rotylenchus*. Cephalic region elevated, offset or continuous, round or truncate anteriorly, finely annulated; anterior annule longitudinally indented into six sectors; labial disc flat, rounded, with six labial pits in two lateral lines near oral aperture; **framework massive, strongly sclerotized in both sexes**. Stylet well developed in both sexes, about 30–44  $\mu\text{m}$  long. Orifice of dorsal oesophageal gland about 3–7  $\mu\text{m}$ , less than one-fourth stylet length behind stylet base. Median bulb behind middle of oesophagus, strongly muscular. **Oesophageal glands short, forming a pyriform terminal bulb** abutting intestine; subventral glands as long as or slightly



**Fig. 66.** A–E. *Rotylenchus* (*Calvatylus*) *calvus* Sher. F–H. *Varotylus* *varus* (Jairajpuri & Siddiqi). I–M. *Rotylenchus* (*Pararotylenchus*) *hopperi* Baldwin & Bell. A. Head end of male. B, G and I. Oesophageal regions of females. C and J. Head ends of females. D, F and K. Tail ends of females. E and M. Tail ends of males. H and L. Basal regions of oesophagus.

longer than dorsal gland; lumen not straight, mostly ventral to the main axis of bulb; cardia absent. Excretory pore opposite glands or at base of isthmus, behind hemizonid. Vulva postmedian ( $V = 52\text{--}65$ ), with non-projecting epitygma. Ovaries paired, outstretched in opposite directions. Spermathecae axial, round to oval. Female tail cylindroid to dorsally convex-conoid, devoid of terminal projection. Male tail conoid, with distinct hyaline terminal portion; bursa enveloping tail tip; phasmids may extend partially into bursa. Spicules cephalated, flanged.

Gubernaculum reflexed distally, with small titillae.

### Type species

*Pararotylenchus brevicaudatus* (Hopper, 1959) Baldwin & Bell, 1981

### Present status

*Rotylenchus* (*Pararotylenchus*) *hopperi* (Baldwin & Bell, 1984) comb. n.  
 syn. *Pararotylenchus hopperi* Baldwin & Bell, 1984, nom. nov. for *Tylenchorhynchus brevicaudatus* Hopper, 1959 (= a junior primary homonym of *Tylenchorhynchus robustus brevicaudatus* Micoletzky, 1922, et Seidenschwarz, 1923 (= *T. robustus typicus* var. *brevicaudatus* Micoletzky, 1922))  
*Pararotylenchus brevicaudatus* (Hopper, 1959) Baldwin & Bell, 1981

### Other species

*Rotylenchus* (*Pararotylenchus*) *belli* (Robbins, 1983) Brzeski & Choi, 1998  
 syn. *Pararotylenchus belli* Robbins, 1983  
*R. (P.) blothrotylus* (Baldwin & Bell, 1981) Brzeski & Choi, 1998  
 syn. *Pararotylenchus blothrotylus* Baldwin & Bell, 1981  
*R. (P.) colocaudatus* (Baldwin & Bell, 1981) Brzeski & Choi, 1998  
 syn. *Pararotylenchus colocaudatus* Baldwin & Bell, 1981  
*R. (P.) flexuosus* (Eroshenko, 1984) Brzeski & Choi, 1998  
 syn. *Pararotylenchus flexuosus* Eroshenko, 1984  
*R. (P.) graminis* (Volkova & Eroshenko, 1995) Brzeski & Choi, 1998  
 syn. *Pararotylenchus graminis* Volkova & Eroshenko, 1995  
*R. (P.) megastylus* (Baldwin & Bell, 1981) Brzeski & Choi, 1998  
 syn. *Pararotylenchus megastylus* Baldwin & Bell, 1981  
*R. (P.) microstylus* (Maqbool, Ghazala, Fatima & Qasim, 1985) Brzeski & Choi, 1998  
 syn. *Pararotylenchus microstylus* Maqbool, Ghazala, Fatima & Qasim, 1985  
*R. (P.) ouensis* Boag & Hooper, 1981  
 syn. *Rotylenchus ouensis* Boag & Hooper, 1981  
*Pararotylenchus ouensis* (Boag & Hooper) Boag & Hooper, 1981  
*R. (P.) pernoxius* (Eroshenko & Kovrizhnykh, 1985) Brzeski & Choi, 1998  
 syn. *Pararotylenchus pernoxius* Eroshenko & Kovrizhnykh, 1985  
*R. (P.) pini* Mamiya, 1968  
 syn. *Rotylenchus pini* Mamiya, 1968  
*Pararotylenchus pini* (Mamiya, 1968) Baldwin & Bell, 1981  
*R. (P.) rarus* (Eroshenko & Kovrizhnykh, 1985) Brzeski & Choi, 1998  
 syn. *Pararotylenchus rarus* Eroshenko & Kovrizhnykh, 1985  
*R. (P.) sphaerocephalus* (Baldwin & Bell, 1981) Brzeski & Choi, 1998  
 syn. *Pararotylenchus sphaerocephalus* Baldwin & Bell, 1981  
*R. (P.) spiralis* (Baldwin & Bell, 1981) Brzeski & Choi, 1998  
 syn. *Pararotylenchus spiralis* Baldwin & Bell, 1981  
*R. (P.) truncocephalus* (Baldwin & Bell, 1981) Brzeski & Choi, 1998  
 syn. *Pararotylenchus truncocephalus* Baldwin & Bell, 1981

## Remarks

Fortuner (1987) stated that *Pararotylenchus* was very close to *Rotylenchus* and, except for the arrangement of the oesophageal glands, there was little to separate the two genera. Some *Rotylenchus* species (e.g. *R. breviglians*) have oesophageal glands forming a pseudobulb with only a short overlap of the intestine and looking similar to that of *Pararotylenchus* spp. A close look, however, shows that the oesophageal lumen is ventral to the oesophageal glands. In *Pararotylenchus*, however, the oesophageal lumen is almost symmetrically arranged between the three oesophageal glands. This small structural difference can not be regarded as a familial character and it was considered by Fortuner (1987) and Maggenti *et al.* (1988) only at the generic level, thereby rejecting Pararotylenchinae. Eroshenko (1984) elevated Pararotylenchinae to family rank and placed it under Tylenchoidea. Brzeski & Choi (1998) synonymized *Pararotylenchus* with *Rotylenchus* and transferred all its species to the latter genus. I consider this sole differentiating character of the oesophageal bulb at the subgeneric level and regard *Pararotylenchus* as a subgenus of *Rotylenchus*. A somewhat similar situation is seen with *Plesiorotylenchus* where a single character of a longitudinally striated head has been used at generic level. Here *Plesiorotylenchus* is also considered as a subgenus of *Rotylenchus*.

ETYMOLOGY. From Greek *para* = beside, near, and *Rotylenchus*.

The type species was found around roots of quaking aspen (*Populus tremuloides* Michx.) in Utah, USA. A key to species was given by Baldwin & Bell (1981).

### Subgenus *Plesiorotylenchus* Vovlas, Castillo & Lamberti, 1993, grad. n.

(Fig. 65, I–N)

## Diagnosis

Genus *Rotylenchus*. No marked sexual dimorphism in anterior region. Cephalic region continuous, truncate, lacking transverse annulation but with **longitudinal striae disposed radially present; labial disc rectangular, prominent; six lip sectors reduced, almost absent**; framework strongly sclerotized. Lateral fields with four incisures. Stylet strong, 45–50  $\mu\text{m}$  long in females and orifice of dorsal oesophageal gland 6–12 (9)  $\mu\text{m}$  behind stylet in type species. Oesophageal glands overlapping intestine dorsally and subdorsally. Didelphic. Tail short, rounded. Phasmids pore-like, near anus level. Bursa enveloping tail, not lobed.

## Type species

*Plesiorotylenchus striaticeps* Vovlas, Castillo & Lamberti, 1993

## Present status

*Rotylenchus* (*Plesiorotylenchus*) *striaticeps* (Vovlas, Castillo & Lamberti, 1993) comb. n.  
No other species.

ETYMOLOGY. From Greek *plesios* = near, and *Rotylenchus*.

The type species was collected from the rhizosphere of grape (*Vitis* sp.) at Osman, Turkey.

**Genus *Orientylus* Jairajpuri & Siddiqi, 1977**

(Fig. 63, A, H &amp; I)

**Diagnosis**

Rotylenchoidinae. Cephalic region small, continuous or slightly offset, smooth or annulated; longitudinal indentations absent; labial disc indistinct. **Orifice of dorsal oesophageal gland more than one-third stylet length behind stylet base. Oesophageal glands overlapping intestine dorsally and dorsolaterally to laterally;** subventral glands symmetrical. **Posterior ovary non-functional or absent;** posterior reproductive tract reduced or represented by a uterine sac. Female tail dorsally convex-conoid to hemispherical, with or without a terminal mucro, under 1.5 anal body widths long. Bursa enveloping tail, not indented terminally. Gubernaculum fixed, lacking titillae. Hypoptygma present.

**Type species**

*Orientylus orientalis* (Siddiqi & Husain, 1964) Jairajpuri & Siddiqi, 1977

syn. *Rotylenchus orientalis* Siddiqi & Husain, 1964

*Helicotylenchus orientalis* (Siddiqi & Husain) Geraert, 1976

**Other species**

*Orientylus desouzai* (Kumar & Rao, 1976) Orton Williams, 1983

syn. *Rotylenchoides desouzai* Kumar & Rao, 1976

*Rotylenchus desouzae* (Kumar & Rao) Fortuner, 1984

*O. geraerti* Jairajpuri & Siddiqi, 1979

syn. *Rotylenchus geraerti* (Jairajpuri & Siddiqi) Zancada & Lima, 1986

*O. impar* (Khan, Saha & Chawla, 1981) Siddiqi, 1986

syn. *Rotylenchoides impar* Khan, Saha & Chawla, 1981

*Helicotylenchus khani* Fortuner, 1984 (= junior objective homonym)

**Nomina nuda**

*Orientylus cognatus* Kapoor, 1983

*O. populus* Kapoor, 1983

*O. prominens* Kapoor, 1983

ETYMOLOGY. From prefix of its type species name *orientalis*, and Greek *tylos* = knob.

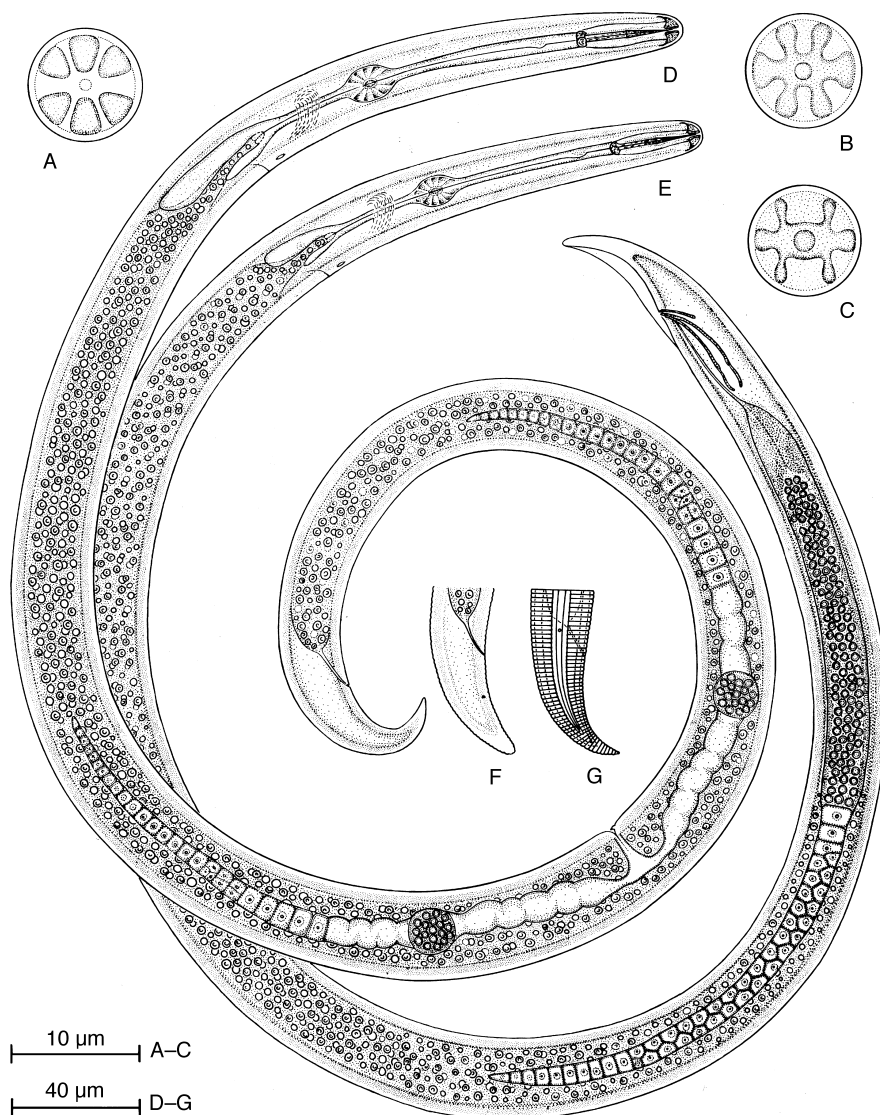
The type species was collected from the soil around roots of *Citrus limonia* (L.) at Shillong, Assam State, India.

**Genus *Antarctylus* Sher, 1973**

(Fig. 67)

**Diagnosis**

Rotylenchoidinae. Body spiral, about 1 mm long, showing poorly marked sexual dimorphism in anterior region. Lateral fields each with four incisures, non-areolated. Deirids absent. Phasmids near anus, preanal in type species. Cephalic region continuous, rounded, finely annulated, lacking longitudinal indentations; framework



**Fig. 67.** *Antarctylus humus* Sher. A. En face view of female. B and C. Cross-sections through basal head annules of female and male, respectively. D. Female. E. Male. F and G. Female tails. (After Sher (1973a), courtesy *Journal of Nematology*.)

strongly sclerotized. Stylet well developed, 27–33 μm long in type species, knobs rounded. Orifice of dorsal gland one-fourth to one-third stylet length behind stylet base. **Oesophageal glands overlapping intestine primarily dorsally**; subventral glands asymmetrical, one located subdorsally, other in its normal position. Oesophago-intestinal valvula distinct. Didelphic. Vulva postmedian. Epitygma

present. Ovaries outstretched. Spermathecae round, axial, with small round sperm. **Female tail regularly tapering, ventrally arcuate**, terminus small, round to pointed, **two to three times anal body width long**. Male tail with long hyaline terminal part. Bursa enveloping tail. Spicules large (30–37  $\mu\text{m}$  in type species), cephalated, slightly arcuate. Gubernaculum linear, apparently non-protrusible.

#### Type species

*Antarctylus humus* Sher, 1973

No other species.

ETYMOLOGY. *Antarktikos* = southern, and *tylos* = knob.

The type species was found in forest peat soil in the subantarctic region on Auckland Island.

### Subfamily Aphasmatylenchinae Sher, 1965

#### Diagnosis

Hoplolaimidae. Body medium-sized, curving ventrally upon relaxation. Poorly marked sexual dimorphism present in anterior region. Lateral fields areolated. Deirids absent. **Phasmids not detectable**. Cephalic region high arched, with conspicuous round labial disc; anterior area divided into six sectors or pseudolips; labial papillae or pits on disc not discernible in SEM. **Amphidial apertures transverse slit-like**, at base of labial disc. Stylet and median bulb well developed in female, slightly less developed in male. Conus of stylet about as long as shaft. Median bulb very muscular. Isthmus elongate-slender. **Oesophageal glands lobe-like, extending over intestine mostly ventrally**. Female tail short, about one-and-a-half anal body widths long; male tail over two anal body widths long, completely enveloped by a simple bursa. Spicules and gubernaculum well developed. Known only from Africa.

#### Type genus

*Aphasmatylenchus* Sher, 1965

No other genus.

#### Remarks

Sher (1965) argued for the inclusion of Aphasmatylenchinae under Hoplolaimidae on the grounds of its having sexual dimorphism in the anterior region, a high-arched well-developed cephalic framework and a labial disc. Elongate male and, to a certain extent, female tails and the dorsal oesophageal gland being somewhat larger than the subventrals bring the Aphasmatylenchinae close to the subfamily Belonolaiminae. However, the labial disc lacking six papillae or pits around the oral aperture, the first head annule being divided into six sectors and sexual dimorphism manifest in the anterior region support its inclusion in the superfamily Hoplolaimoidea. The ventrally overlapping oesophageal glands show a tendency towards the types of glands found in some Hoplolaimoidea. Fotedar & Handoo (1978) raised Aphasmatylenchinae to family rank.

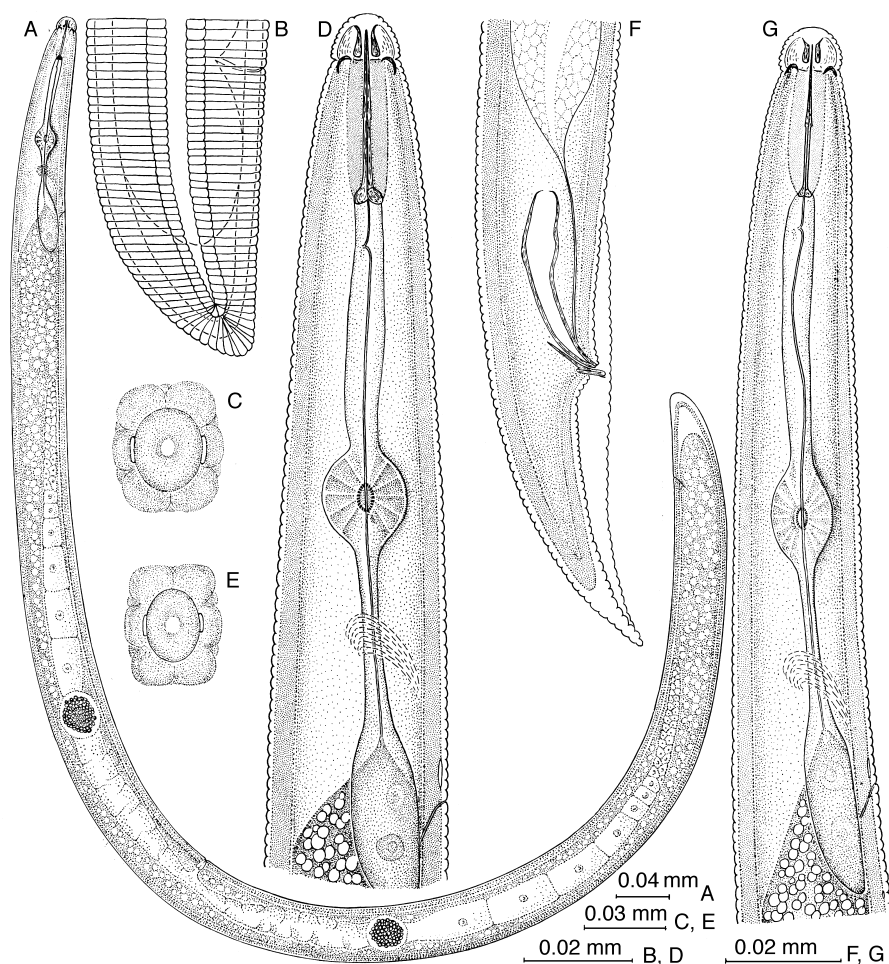


## Genus *Aphasmatylenchus* Sher, 1965

(Figs 59, B; 68)

### Diagnosis

Aphasmatylenchinae. Medium-sized (0.9–1.75 mm), with poorly marked sexual dimorphism in anterior region. Annules prominent, smooth, or marked with closely spaced longitudinal striae. Lateral fields each with four incisures, areolated. Deirids absent. **Phasmids not detectable**. Cephalic region offset by constriction, annulated; labial disc distinct, rounded; framework with high arches; moderately to strongly sclerotized. Stylet well developed, less than three cephalic region widths long, 29–32  $\mu\text{m}$  long in females of type species; knobs rounded. Orifice of dorsal gland at



**Fig. 68.** *Aphasmatylenchus nigeriensis* Sher. A. Female. B. Tail end of female. C and E. En face views of female and male, respectively. D. Oesophageal region of female. F. Tail end of male. G. Oesophageal region of male. (After Sher (1965), courtesy Helminthological Society of Washington.)

about one-fourth stylet length behind stylet base. **Oesophageal glands forming a lobe overlapping anterior end of intestine mostly ventrally**; dorsal gland nucleus larger than those of subventrals. Excretory pore and hemizonid near base of oesophagus. Vulva equatorial. Spermathecae round, axial. Ovaries paired, outstretched. Female tail cylindroid to conoid-rounded, about one-and-a-half anal body widths long. Intestine with serpentine fasciculi extending over rectum into tail cavity. Male tail conical, over two anal body widths long, completely enveloped by a bursa having finely crenate edges. Spicules large (31–36  $\mu\text{m}$  in type species), cephalated, slightly flanged distally. Gubernaculum well developed, modified, protrusible.

#### Type species

*Aphasmatylenchus nigeriensis* Sher, 1965

#### Other species

*Aphasmatylenchus straturatus* Germani, 1970

*A. liberiensis* Baujard, Vovlas, Mounport & Martiny, 1998

*A. variabilis* Germani & Luc, 1984

ETYMOLOGY. From Greek *a* = privative prefix, *phasma* = phasid, and *Tylenchus*.

The type species was found around roots of *Theobroma cacao* and *Hevea brasiliensis* in Nigeria. It was also found in forests of French Guiana. *Aphasmatylenchus straturatus* and *A. variabilis* occurred around roots of *Arachis hypogaea* L. in Upper Volta and Senegal, respectively.

## FAMILY ROTYLENCHULIDAE

### (Ectoparasitic Hoplolaimoidea with sausage- or kidney-shaped mature females)

This family represents a transitional stage between a vermiform migratory ectoparasite and a saccate sedentary endoparasite. The female, although an ectoparasite, is capable of feeding on deeper root tissue, ensuring a continuous supply of food by inciting the host to produce transfer cells or giant cells in the vicinity of its head. This demonstration of advanced root parasitism provides an indication of the evolution to the most advanced root-parasitic Tylenchida, the Heteroderidae. The discovery of *Meloinema* (Choi & Geraert, 1974), *Bursadera* (Ivanova & Krall, 1985), *Verutus* (Esser, 1981) and *Bilobodera* (Sharma & Siddiqi, 1992) made it possible to link *Rotylenchulus* and *Senegalonema* (Hoplolaimidae) to *Meloidogyne* (Meloidogynidae) and to *Meloidodera* and *Hylonema* (Heteroderidae).

The ventral overlapping of the oesophageal glands, so consistently found in the Heteroderidae, is seen in the Rotylenchulinae and also in the Pratylenchinae and Rotylenchoidinae of the Hoplolaimoidea. The development of the Heteroderidae from the Hoplolaimoidea-like forms can best be traced via the forms similar to the members of the Rotylenchulinae rather than through the Hoplolaiminae, Radopholinae or Nacobbiniae, which have dorsally overlapping glands (see Wouts & Sher, 1971; Husain, 1976). The possibility remains for the development of the

Heteroderidae from groups other than those similar to Rotylenchulinae, whether known or unknown. One example of this possibility can be found in the present-day *Belonolaimus* and *Aphasmatylenchus* which show a tendency to a ventral shifting of the oesophageal glands. The well-developed cephalic sclerotization, stylet and oesophagus in males of the Heteroderidae and Meloidogynidae are in contrast to the Rotylenchulidae, in which the males show a degree of reduction in the development of these structures.

In the character of the oesophageal glandular overlap, the reduction of the tail in the females and males, and in the shape of the tail of its early stage juveniles, *Verutus* closely approximates the members of the Heteroderidae, but the genus is ectoparasitic in habit and has an elongated postvulval region of the female body which, as a whole, is not spheroidal, eggs are laid as they mature, and the male stylet is reduced and less developed than that in the females or juveniles. The reduction of the male tail and the absence of a bursa in *Verutus* is a direct result of the absence of a slender female stage in this genus. *Bilobodera* also lacks a slender female stage and is close to *Verutus*, differing in the bilobed shape of the female body, cephalic framework lacking conspicuous sclerotization and a different face view.

The genus *Rotylenchulus* is indigenous mainly in the Ethiopian region, where most of its speciation seems to have occurred. *Rotylenchulus reniformis* is very widely distributed throughout the tropical and subtropical countries, parasitizing a number of cultivated plants and fruit trees. The nematode is a serious problem to field crops, such as potato, maize, soybean, cotton and pineapple. In Hawaii, it has built up such large populations in pineapple fields that the entire pineapple industry of Hawaii is threatened. Soil fumigants applied to check populations have contaminated subsoil water and hence their use is discouraged and banned.

*Rotylenchulus reniformis* is capable of developing from egg to adult in water, without feeding, and growth through a series of at least three superimposed moults, the first of which occurs within the egg. Adult males and immature females, of about the same length as newly hatched juveniles, are produced in equal numbers. The immature female finds a suitable host and feeds ectoparasitically on deeper root tissues, such as cortex, pericycle and phloem, where a large number of giant cells are formed by the host. The posterior part of the body soon swells to become kidney-shaped and eggs are laid within 7–9 days in a gelatinous matrix, forming egg masses of about 50 eggs each. The life cycle is completed in 17–29 days (see details in Siddiqi, 1972).

*Rotylenchulus reniformis* can survive in dried soil for several months when soil moisture recedes gradually. But alternate hydration and dehydration, as in irrigation and summer ploughing, has been shown to reduce the survival of nematodes more than the continuous moist or dry regimes (Sehgal & Gaur, 1995). It penetrates roots intracellularly and induces giant cell formation near the stele or on the pericycle. A feeding peg is formed on the cell adjacent to the nematode head, and a helically coiling feeding tube (apparently formed by the solidification of the extruded salivary secretion) appears within the feeding cell. A continuous flow of the cell solutes is maintained through this feeding tube (Razak & Evans, 1976; Rebois, 1981; see Fig. 15, B). Nematode feeding results in intense hypertrophy and hyperplasia in the phloem tissues.

*Rotylenchulus macrodoratus* parasitizes pistachio and large-flowered sweet william,

and causes hyperplasia of the secondary parenchymal cells surrounding the uninucleate giant cells. The root in this region appears galled (Vovlas, 1983a). *Rotylenchulus parvus* is widespread in eastern and southern Africa, attacking barley, beans, cowpea, grasses, sugarcane and sweet corn. It lays 14–37 eggs in a gelatinous matrix, the first moult occurring within the egg in 5 to 8 days after the first cleavage. The second-stage juveniles do not feed but develop to immature females through three superimposed moults, whether held in water, in soil or on agar. The entire life cycle from egg to egg takes 27–36 days (Dasgupta *et al.*, 1968).

*Verutus volvingentis* attacks buttonweed (*Diodia virginiana* L.) in Florida, USA. The third-stage juvenile becomes slightly obese while feeding ectoparasitically on roots, and develops into the swollen female *in situ*, without a migratory stage. The mature female becomes sausage- to kidney-shaped and lays eggs singly (not in groups or forming egg masses) as they mature, in a gelatinous matrix. *Senegalonema sorghi* has a migratory immature female found in soil, which feeds ectoparasitically on roots of sorghum and the exposed part of the body becomes saccate, generally kidney-shaped. *Acontylus vipriensis* parasitizes roots of *Eucalyptus* sp., *Acacia* sp. and grass in Australia. It is also ectoparasitic, but the female body swells to a lesser degree than that in *Rotylenchulus* or *Verutus*. The nematode lays eggs in a gelatinous matrix and forms colonies on the roots (Meagher, 1968, 1976).

The subfamily Rotylenchulinae was considered under the family Nacobbidae by Golden (1971), but Siddiqi (1971) classified it under the Hoplolaimidae close to the Rotylenchoidinae and assigned Nacobbinae to the family Pratylenchidae. The swelling of the female body appears to have occurred independently in Rotylenchulinae and Nacobbinae; the former seems to have evolved from ectoparasitic forms and the latter from endoparasitic ones, as is reflected by the biology of their juveniles. Rotylenchulidae is close to Rotylenchoidinae of the Hoplolaimidae not only in the arrangement of the oesophageal glands with respect to the intestine, but also in the structure of the cephalic region, stylet, and in SEM face views (inner labial papillae not on surface, amphidial aperture slit-like). There is also a similarity in the regression of the cephalic sclerotization and stylet in the males of the two groups. The dorsally subterminal spicular pore is similar in both *Rotylenchulus* and *Helicotylenchus* and is also found in *Pratylenchus* and *Hirschmanniella* (Geraert & De Grisse, 1982).

Rotylenchulinae, Verutinae and Acontylinae are here recognized under Rotylenchulidae, as separate subfamilies on the basis of their representing distinct evolutionary lines, as indicated by their ontogeny and morphology. In Rotylenchulinae, the juvenile tail is more rounded and its hyaline terminal portion less prominent (cf. Pratylenchinae or Rotylenchoidinae) than in females and there is a vermiform, migratory immature female stage, whereas in Verutinae the juvenile tail in early stages is elongate-conoid, becoming rounded in later stage(s) (cf. Acontylinae and *Hoplolaimus concaudajuvencus*), and there is no vermiform immature female stage. Acontylinae is characterized by sexual dimorphism and oesophageal gland arrangement similar to Radopholinae, but its juveniles and adults are ectoparasitic in habit and have the orifice of the dorsal oesophageal gland located far behind the stylet base. The family Rotylenchulidae represents an intermediate stage between the Hoplolaimidae and Meloidogynidae/Heteroderidae. Thus there seems to be good justification for uniting Hoplolaimidae, Pratylenchidae,

Rotylenchulidae, Heteroderidae and Meloidogynidae under Hoplolaimoidea and not recognizing the superfamily Heteroderoidea.

## Family Rotylenchulidae Husain & Khan, 1967 (Husain, 1976)

### Diagnosis

Hoplolaimoidea. Small-sized, about 1 mm or less long, with **marked sexual dimorphism in adult body shape and in anterior region**. **Mature female swollen**, often sausage- or kidney-shaped behind a less swollen neck; immature female vermiform in type genus. **Male vermiform, with reduced cephalic sclerotization, stylet and oesophagus**. Cuticle annulated. Lateral field with four incisures, not areolated. Cuticle annulation and lateral field obliterated in mature female. Deirids absent. **Phasmids pore-like, on tail near anus**. **Cephalic region in female high, rounded to truncate**, continuous or rarely offset, lacking longitudinal indentations; sclerotization strong in females and juveniles. Excretory pore in oesophageal region. Stylet in female and juveniles well developed, two to three cephalic region widths long, conus about as long as or shorter than shaft, knobs prominent, rounded; **male stylet weaker than that of female**. Orifice of dorsal oesophageal gland often well separated from base of stylet. Median oesophageal bulb muscular, with large refractive thickenings. Oesophageal glands extending over intestine mostly ventrally or, as in Acontylinae, dorsally. Vulva postmedian or more posterior, with round lips; lateral membranes absent. Ovaries reflexed, coiled or straight. Tail in mature female present, or rudimentary but a distinct postvulval region of body always present. Male tail conoid or reduced (*Verutus*); bursa present or absent. Testis single, outstretched. Spicules cephalated, ventrally arcuate, with narrow distal tip having a dorsally subterminal pore and lacking distinct flanges. Gubernaculum large, trough-shaped, fixed. **Juveniles** vermiform (except later stages of *Verutus*), with distinct or indistinct hyaline terminal portion of tail, straight, **ventrally arcuate or curved when relaxed**. Eggs laid singly in gelatinous matrix, not retained in body in large numbers. **Adult female a sedentary ectoparasite of roots**.

### Type subfamily

Rotylenchulinae Husain & Khan, 1967

### Other subfamilies

Acontylinae Fotedar & Handoo, 1978

Verutinae Esser, 1981

### Key to subfamilies of Rotylenchulidae

1. Female and male with distinct tails, young vermiform migratory female stage present; bursa present ..... 2  
 Female and male with very reduced tails, young vermiform migratory female stage absent; bursa absent ..... **Verutinae**
2. Oesophageal glands mostly dorsal to intestine; one functional ovary; male head inflated; juveniles almost straight on death ..... **Acontylinae**  
 Oesophageal glands mostly ventral to intestine; two functional ovaries; male head not inflated; juveniles curved on death ..... **Rotylenchulinae**

## Subfamily Rotylenchulinae Husain & Khan, 1967

syn. Rotylenchulinae Allen & Sher, 1967

(Leiperotylenchinae in Skarbilovich, 1980 = nomen nudum)

### Diagnosis

Rotylenchulidae. Small-sized (usually 0.5 mm or under). **No marked sexual dimorphism in body shape in young females and males**; only mature female saccate or kidney-shaped. Cephalic region high, continuous, with or without distinct annules. Cephalic sclerotization, stylet and median oesophageal bulb well developed in juveniles and females, regressed in males. **Male stylet weaker than that of female**. Oesophageal glands in juveniles elongated, **overlapping intestine mostly ventrally or laterally**. Didelphic, ovaries reflexed or coiled in mature female. **Young female and male tails similar** in being elongate-conoid and having a long hyaline terminal portion; **tail persists in mature swollen female**. Bursa present, low. Juveniles ventrally curved on death, tails tapering to a round tip, two to three anal body widths long, hyaline terminal portion smaller than that in young female and in male.

### Type genus

*Rotylenchulus* Linford & Oliveira, 1940

### Other genus

*Senegalonema* Germani, Luc & Baldwin, 1984

### Key to genera of Rotylenchulinae

1. Dorsal oesophageal gland orifice at less than half stylet length behind stylet base; young female with outstretched ovaries; bursa enclosing tail tip .....*Senegalonema*
- Dorsal oesophageal gland orifice at more than half stylet length behind stylet base; young female with ovaries having double flexures; bursa not enclosing tail tip ..... *Rotylenchulus*

### Genus *Rotylenchulus* Linford & Oliveira, 1940

syn. *Leiperotylenchus* Das, 1960

*Spyrotylenchus* Lordello & Cesnik, 1958

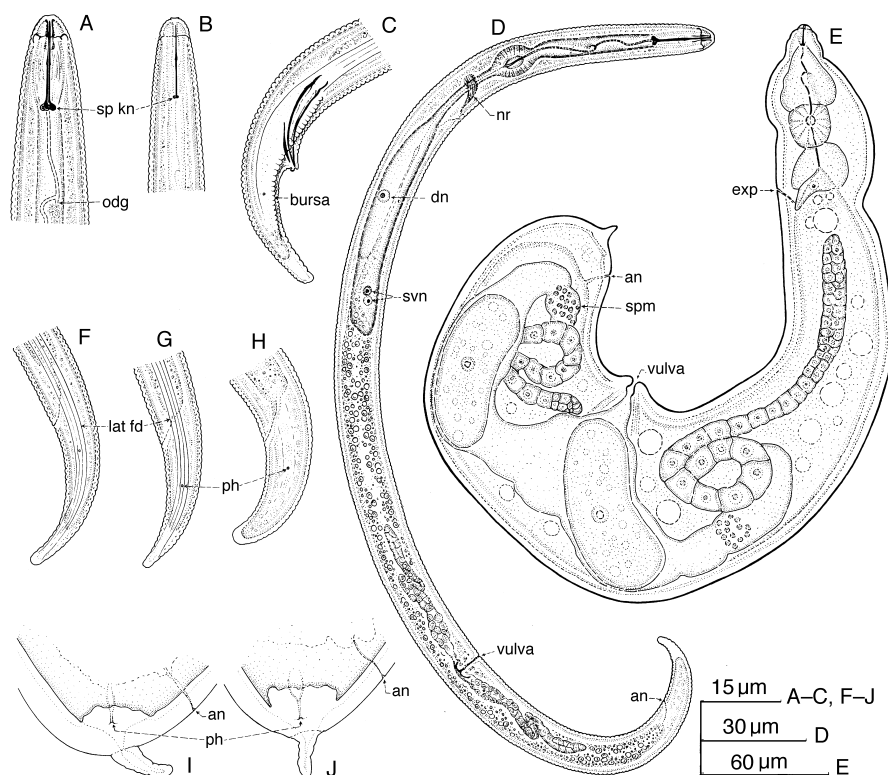
(*Spirotylenchus* in Lordello & Cesnik, 1958

= *lapsus calami*, incorrect original spelling)

(Fig. 69)

### Diagnosis

Rotylenchulinae. Juveniles, males and **young females vermiform, arcuate to spiral upon relaxation**. Mature female kidney-shaped, with an irregular, less swollen neck, a postmedian vulva and **a short pointed tail**. Cuticle annulated. Lateral fields each with four incisures, non-areolated, obliterated in mature female. Cephalic region high, continuous. Stylet in juveniles and female two to three times cephalic region width long. **Orifice of dorsal oesophageal gland usually about one stylet length behind stylet base**. Subventral glands in the normal position, dorsal gland shifted laterally to subventrally, former much longer than the latter. **Immature female: Vermiform, migratory** (has been mistaken for adult stage and formed the basis for



**Fig. 69.** *Rotylenchulus reniformis* Linford & Oliveira. A and F–G. Head end and tail ends of immature females, respectively. B and C. Head end and tail end of male, respectively. D. Entire immature female. E. Entire mature female. H. Tail end of juvenile. I and J. Tail ends of mature females. an, anus; dn, dorsal gland nucleus; exp, excretory pore; lat fd, lateral field; nr, nerve ring; odg, orifice of dorsal gland; ph, phasmid; sp kn, spear knobs; spm, spermatheca; svn, subventral gland nuclei. (A–D and F–J. After Siddiqi (1972). E. After Dasgupta *et al.* (1968).)

the proposal of new genera, *Spyrotylenchus*, *Leiperotylenchus*). Ovaries paired, with double flexures. Tail elongate-conoid, with prominent hyaline terminal portion.

**Male:** Stylet and oesophagus regressed. Tail similar to that of young female; **bursa subterminal, low**, not quite projecting beyond tail contour in lateral view (hence mistakenly reported absent in *R. stakmani* (= *R. reniformis*)). Phasmids located on tail in its anterior region. Spicules slender, lacking distal flanges. Gubernaculum fixed, devoid of titillae and telamon. Cloacal lips pointed, not forming a tube; hypopygium absent. Juvenile tail more rounded terminally and with shorter hyaline terminal portion than that of female.

### Type species

- Rotylenchulus reniformis* Linford & Oliveira, 1940  
 syn. *Tetylenchus nicotiana* Yokoo & Tanaka in Tanaka & Tsumagori, 1954  
*Rotylenchulus nicotiana* (Yokoo & Tanaka in Tanaka & Tsumagori) Baker, 1962 (Nakasono & Ichinohe (1967) and Dasgupta *et al.* (1968) also proposed this combination)  
*Rotylenchus elisensis* Carvalho, 1957  
*Helicotylenchus elisensis* (Carvalho) Carvalho, 1959  
*Rotylenchulus elisensis* (Carvalho) Siddiqi, 1986  
*Spyrotylenchus queirozi* Lordello & Cesnik, 1958  
*Rotylenchulus queirozi* (Lordello & Cesnik) Sher, 1961  
*Leiperotylenchus leiperi* Das, 1960  
*Rotylenchulus leiperi* (Das) Loof & Oostenbrink, 1961  
*Rotylenchulus stakmani* Husain & Khan, 1965

### Other species

- Rotylenchulus anamictus* Dasgupta, Raski & Sher, 1968  
*R. borealis* Loof & Oostenbrink, 1962  
*R. brevitubulus* Van den Berg, 1990  
*R. clavicaudatus* Dasgupta, Raski & Sher, 1968  
*R. leptus* Dasgupta, Raski & Sher, 1968  
*R. macrodoratus* Dasgupta, Raski & Sher, 1968  
*R. macrosoma* Dasgupta, Raski & Sher, 1968 (original spelling *macrosomus*)  
*R. parvus* (Williams, 1960) Sher, 1961  
 syn. *Helicotylenchus parvus* Williams, 1960  
*R. sacchari* Van der Berg & Spaull, 1981  
*R. variabilis* Dasgupta, Raski & Sher, 1968

### Note

*Rotylenchulus macrosoma* is generally similar to *R. borealis* in morphology, host preference and host tissue reaction. By its feeding, *R. macrosoma* incites hypertrophy of pericycle cells which form a syncytium. A feeding tube within the enlarged feeding cell is formed. *Rotylenchulus macrodorus*, on the other hand, incites a single uninucleate giant cell within the host tissue (Cohn & Mordechai, 1988).

ETYMOLOGY. Latin diminutive of *Rotylenchus*.

The type species was found parasitizing cowpea (*Vigna sinensis* Endl.) on the Island of Oahu, Hawaii, USA.

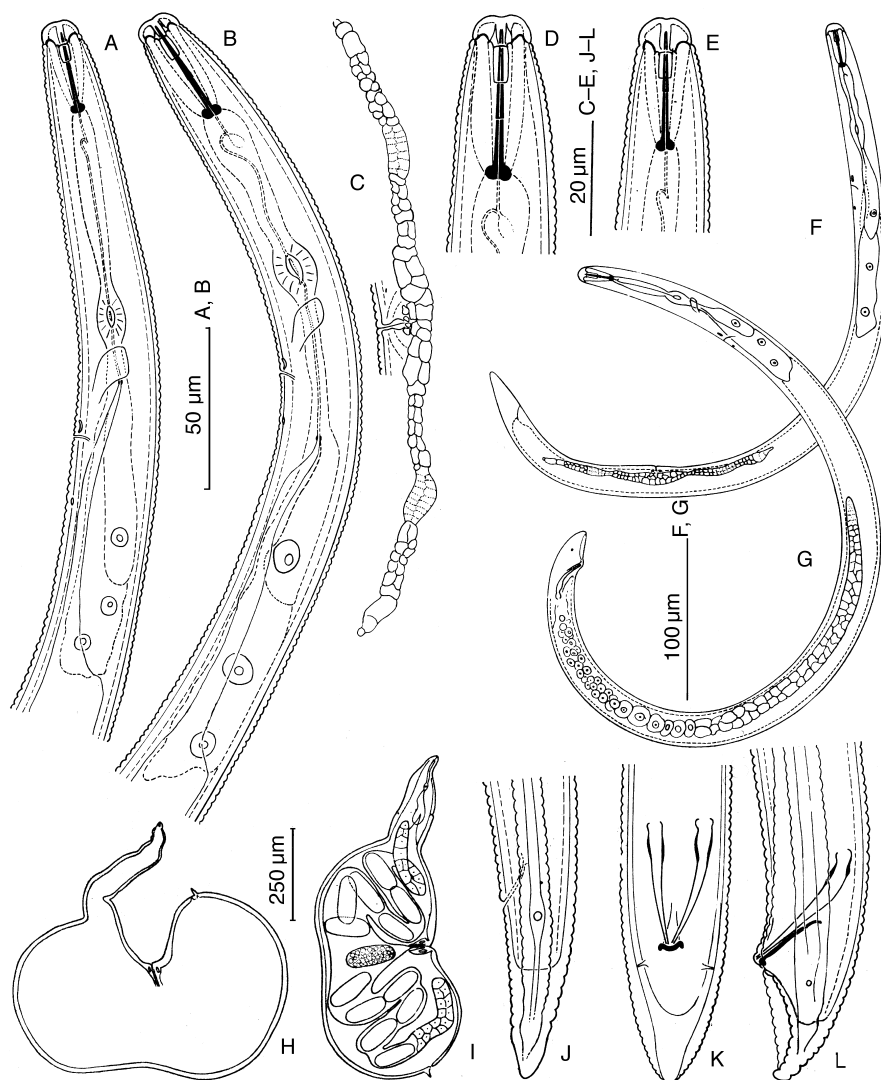
### Genus *Senegalonema* Germani, Luc & Baldwin, 1984

(Fig. 70)

### Diagnosis

Rotylenchulinae. Small-sized (immature females and males 0.35–0.55 mm long, a = 16–29; mature females may grow up to 0.78 mm long), ventrally curved when relaxed. Cuticle annulated. Lateral fields originating just behind lateral pseudolips,





**Fig. 70.** *Senegalonema sorghi* Germani, Luc and Baldwin. A and B. Oesophageal regions of young females. C. Genital tracts of young female. D and E. Head ends of young female and male, respectively. F. Young female. G. Male. H and I. Mature females *in toto*. J. Tail end of young female. K and L. Ventral and lateral views of male tails, respectively. (After Germani *et al.* (1984), courtesy *Revue de Nématologie*.)

each with four incisures, outer bands faintly areolated in oesophageal and tail regions. Phasmids prominent. Cephalic region smooth, continuous, broadly rounded to flat anteriorly. In SEM, labial disc appears lemon-shaped or oval, being fused with submedian pseudolips, which appear triangular with apex of triangle extending to level of basal plate; lateral pseudolips trapezoid; labial papillae at the very edge of

inside margins of oral opening. **Mature female:** Body annulated, swollen posteriorly, kidney-shaped or saccate, usually with a slight constriction at vulval level; anterior region irregular, vermiform. Lateral fields not seen. Cephalic sclerotization weak. Stylet slender, 17–23  $\mu\text{m}$  long; **orifice of dorsal gland at less than half stylet length from stylet base.** Median bulb strongly developed. Excretory pore opposite oesophageal glands. Vulva post-equatorial, lips not protruding. The two branches of the reproductive organs convoluted. Several eggs in each uterus; eggs laid in a gelatinous matrix. **Immature female:** Vermiform. Stylet strong, 22–28  $\mu\text{m}$  long, basal knobs rounded, closely adpressed to the shaft. Orifice of dorsal gland 5–7  $\mu\text{m}$  behind stylet base. Median bulb oval, strongly muscular. Oesophageal glands filling pseudocoelom, extending over intestine laterally or ventrally, more often laterally; dorsal gland smaller than and anterior to subventrals. Vulva at 70–76%, lips not protruding. **Ovaries outstretched**, under-developed. Intestine lacking fasciculi, not extending over rectum. **Tail conical**, annulated, 24–32  $\mu\text{m}$  or about 1.5–2.5 times anal body width long, terminal hyaline portion 51–81% of total tail length in type species. Phasmids 1.5  $\mu\text{m}$  in diameter, at 1–4  $\mu\text{m}$  behind anal level. **Male:** Stylet 18–21.5  $\mu\text{m}$  long, shorter than that of female. Oesophagus less developed than in female, but not degenerate. **Tail conoid**, ventrally arcuate, less than two anal body widths long, **completely enveloped by a low bursa.** Spicules pointed distally, 23–32.5  $\mu\text{m}$  long. Gubernaculum straight, **with titillae**, not protrusible, 9–13.5  $\mu\text{m}$  long in type species.

#### Type species

*Senegalonema sorghi* Germani, Luc & Baldwin, 1984

No other species.

#### Remarks

Germani *et al.* (1984) considered *Senegalonema* and *Rotylenchulus* as pertaining to the family Hoplolaimidae and constituting the subfamily Rotylenchulinae. They pointed out that both genera suggest a morphological link between the Hoplolaimidae and Meloidogyninae. *Senegalonema* differs from *Rotylenchulus* in having a different face view, especially in the structure and fusion of the labial disc with pseudolips, orifice of dorsal oesophageal gland located at less than one half stylet length behind the stylet base, outstretched ovaries in young female, the bursa enclosing the tail tip, and the gubernaculum with titillae.

ETYMOLOGY. From Senegal, country of its original occurrence, and *nema* = nematode.

Type species parasitizes *Sorghum* sp., near Patar, Senegal.

## Subfamily Verutinae Esser, 1981

### Diagnosis

Rotylenchulidae. Small to moderate-sized (0.3–1 mm). Female saccate, with a long neck, sausage- or kidney-shaped posteriorly (*Verutus*) or bilobed with a sharp dorsal depression opposite the median vulva (*Bilobodera*), male vermiform; **no vermiform young female stage**. Body annulation distinct, even in swollen females. **Male stylet weaker than that of female**. Oesophageal gland lobe short, mostly ventral to intestine. Vulva uncommonly large, cleft-like, median or postmedian, lips protuberant. Ovaries doubly reflexed or coiled. **Female anus and cloacal aperture subterminal**. **Tail in adults rudimentary, obtuse**. Juveniles in early stage with elongate-conoid tail having a long hyaline terminal portion, in last stage tail becoming rounded.

### Type genus

*Verutus* Esser, 1981

### Other genus

*Bilobodera* Sharma & Siddiqi, 1992

### Key to genera of Verutinae

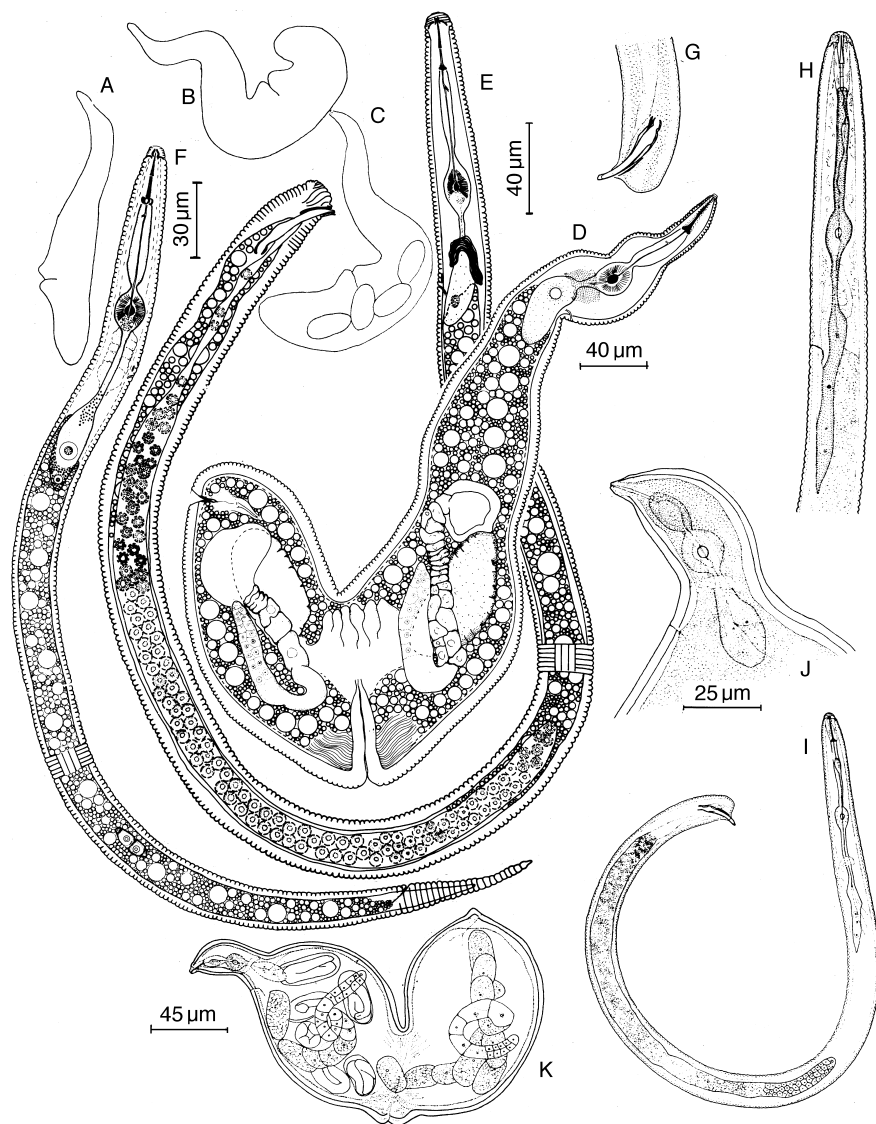
1. Female body bilobed, cephalic framework in all stages weakly sclerotized ..... *Bilobodera*  
     Female body not bilobed, cephalic framework in all stages strongly  
     sclerotized ..... *Verutus*

### Genus *Verutus* Esser, 1981

(Fig. 71, A–F)

### Diagnosis

Verutinae. **Female:** Reniform or sausage-shaped, usually more enlarged on dorsal side. Neck irregular in outline but less swollen, occasionally reflexed across the posterior body; lateral field irregular or as interruption of annules, or indistinct. Cuticle 9–10  $\mu\text{m}$  thick, evenly striated, striae about 2.5  $\mu\text{m}$  apart. Cephalic region offset, with two annules. Stylet about 23–29  $\mu\text{m}$ , knobs 4–5  $\mu\text{m}$  across. Orifice of dorsal gland 7–11  $\mu\text{m}$  behind stylet base. Median bulb well developed. Isthmus and gland lobe short. Vulva about 62  $\mu\text{m}$  long, with round protuberant lips. Ovaries reflexed. Anus subterminal forming small depression. Tail vestigial or absent. Phasid not detectable. **Male:** Body 0.65–1 mm long. Annules about 2  $\mu\text{m}$  wide. Lateral fields each with four incisures, not areolated. Cephalic region annulated, not offset, strongly sclerotized. Amphids indistinct, aperture crescent-like, on posterior margin of lateral lip areas. Stylet 21–27  $\mu\text{m}$  long, weaker than that of females and juveniles. Median bulb with distinct refractive thickenings, slightly longer than that of female. Gland lobe with a distinct nucleus. Cloacal lips form a short penial tube. Bursa absent. Testis outstretched. Spicules slightly arcuate, cephalated, 36–47  $\mu\text{m}$  long. Gubernaculum 15–19  $\mu\text{m}$  long. **Juveniles:** First- and second-stage juveniles 0.43–0.54 mm long, with well-developed cephalic sclerotization, stylet (21–25  $\mu\text{m}$  long) and oesophagus. **Tail elongate-conoid**, four to six anal body widths long, **with**



**Fig. 71.** A–F. *Verutus volvingentis* Esser. G–K. *Bilobodera mesoangusta* (Minagawa) Sharma & Siddiqi. A–D and K. Females. E and I. Males. F. First-stage juvenile. G. Tail end of male. H and J. Oesophageal region of male and female, respectively. (A–F. After Esser (1981); G–K. After Minagawa (1986).)

**hyaline portion longer than protoplasmic part.** Third-stage juvenile with a rounded tail. Phasmids detectable only in early-stage juveniles in anterior region of tail.

**ETYMOLOGY.** From Latin *verutus* = armed with a javelin.

The type species was found on *Diodia virginiana* L. (buttonweed) in Florida, USA.

## Type species

*Verutus volvingentis* Esser, 1981

## Other species

*Verutus californicus* Baldwin, Bernard & Mundo-Ocampo, 1989

## Note

Carta & Baldwin (1990) pointed out that the opening of the ampulla of the phasmid relative to its depth is wide in *Scutellonema*, *Hoplolaimus* and *Meloidodera* and narrow in *Rotylenchus*, *Verutus* and *Heterodera*. They argued that the phasmid in *Verutus* is more similar in structure and shape to *Heterodera* than to *Meloidodera* and hence *Verutus* and *Meloidodera* are not a monophyletic group as upheld by Ferris (1985).

**Genus *Bilobodera* Sharma & Siddiqi, 1992**

(Fig. 71, G–K)

## Diagnosis

Verutinae. **Female:** **Body bilobed** (hence the generic name), with a sharp dorsal depression opposite the median vulva. Cuticle striated. Two ovaries coiled within the two lobes of the swollen body. Eggs generally retained in the body. Immature slender female stage absent. Cyst stage absent. Stylet 14.5–19.0  $\mu\text{m}$  long in type species, with distinct knobs. Vulva a long slit, median, with round protuberant lips. Anus subterminal forming small depression. Tail vestigial or absent. Phasmid not detectable. **Male:** Body under 0.6 mm long, C-shaped when fixed; posterior end not twisted. Stylet small, under 20  $\mu\text{m}$ . Spicules with a truncate, or indented tip. Gubernaculum linear, lacking titillae, fixed. **Tail almost absent**, a hemispherical post-anal region of body present. **Bursa absent.** **Juveniles:** Second-stage juveniles 0.29–0.38 mm long, straight to arcuate when relaxed. Lateral field with four incisures. Cephalic region rounded, continuous, with three to four annules; sclerotization weak. Stylet small, under 17  $\mu\text{m}$ . Orifice of dorsal oesophageal gland about half stylet length behind stylet. Oesophageal glands ventral to intestine. **Tail elongate-conoid with an attenuated and conspicuous hyaline terminal portion.** Phasmids punctiform, a little below anus level but anterior to middle of tail.

## Type species

*Bilobodera mesoangusta* (Minagawa, 1986) Sharma & Siddiqi, 1992  
syn. *Verutus mesoangustus* Minagawa, 1986

## Other species

*Bilobodera flexa* Sharma & Siddiqi, 1992

ETYMOLOGY. From Latin, *bis* = two, and Greek, *lobos* = lobe, *deras* = skin.

The type species was found associated with *Miscanthus sinensis* Anderss. at Yatabe, Ibaraki Prefecture, Japan. It was also found on Mt Aso in Kumamoto Prefecture, Japan (Minagawa, 1986). *Bilobodera flexa* was collected from soil and roots of *Allmania nodiflora* (L.) (Amaranthaceae) in Andhra Pradesh, India.

## Subfamily Acontylinae Fotedar & Handoo, 1978

### Diagnosis

Rotylenchulidae. **Pronounced sexual dimorphism in cephalic region.** Mature female slightly obese posteriorly. Male stylet and oesophagus regressed. Migratory immature female stage present. **Juveniles and immature female straight to slightly arcuate when relaxed. Oesophageal glands overlapping intestine mostly dorsally. Pseudo-mono-prodelphic.** Ovary outstretched. Female tail subcylindroid, obtusely rounded. Juveniles tail tapering, narrowly rounded, with conspicuous hyaline terminal region. Bursa enveloping entire tail.

### Type genus

*Acontylus* Meagher, 1968

No other genus.

### Remarks

Among the Rotylenchulidae, the nematodes of this subfamily are peculiar in having immature females straight to arcuate when relaxed, oesophageal glands overlapping intestine dorsally, anterior ovary outstretched, posterior reproductive branch degenerated and male head inflated to become knob-like. The oesophageal glands, male head and body shape are reminiscent of Radopholinae, while the characters of ectoparasitism and of the orifice of the dorsal gland being located well behind the stylet base point to its affinities with the members of the Rotylenchoidinae. The ectoparasitism in which the female swollen posterior part remains outside the root, the existence of a vermiform immature female stage, the position of the dorsal gland orifice, the regression of the male stylet and oesophagus and the eggs laid singly in gelatinous matrix justify the inclusion of Acontylinae in the family Rotylenchulidae.

### Genus *Acontylus* Meagher, 1968

(Fig. 72)

### Diagnosis

Acontylinae. Small-sized (under 1 mm), **straight to arcuate upon relaxation.** Sexual dimorphism in anterior region present. Immature female slender, mature female slightly swollen posteriorly. Cuticle finely annulated. Lateral fields each with four incisures, not areolated. Deirids absent. Phasmids in anterior region of tail, in male extending into bursa. Amphidial apertures labial, indistinct. Female cephalic region conoid-rounded, offset, annulated; framework heavily sclerotized, outer margins conspicuous; labial disc indistinct; **male cephalic region high and broadly rounded, knob-like**, with reduced sclerotization. Stylet in female robust (19–22  $\mu\text{m}$  long in type species), with large amalgamated knobs, in male reduced in size (17–18  $\mu\text{m}$  long in type species). **Orifice of dorsal oesophageal gland more than half stylet length behind stylet base.** Postcorporate bulb strongly muscular in female (reduced in male), with distinct cuticular thickenings, offset from precorpus. **Oesophageal glands elongate, overlapping intestine dorsally and dorsolaterally.** Excretory pore opposite isthmus, behind hemizonid. Vulva at 82–85% of body length. Postvulval uterine sac one to two body widths long, terminus annulated.

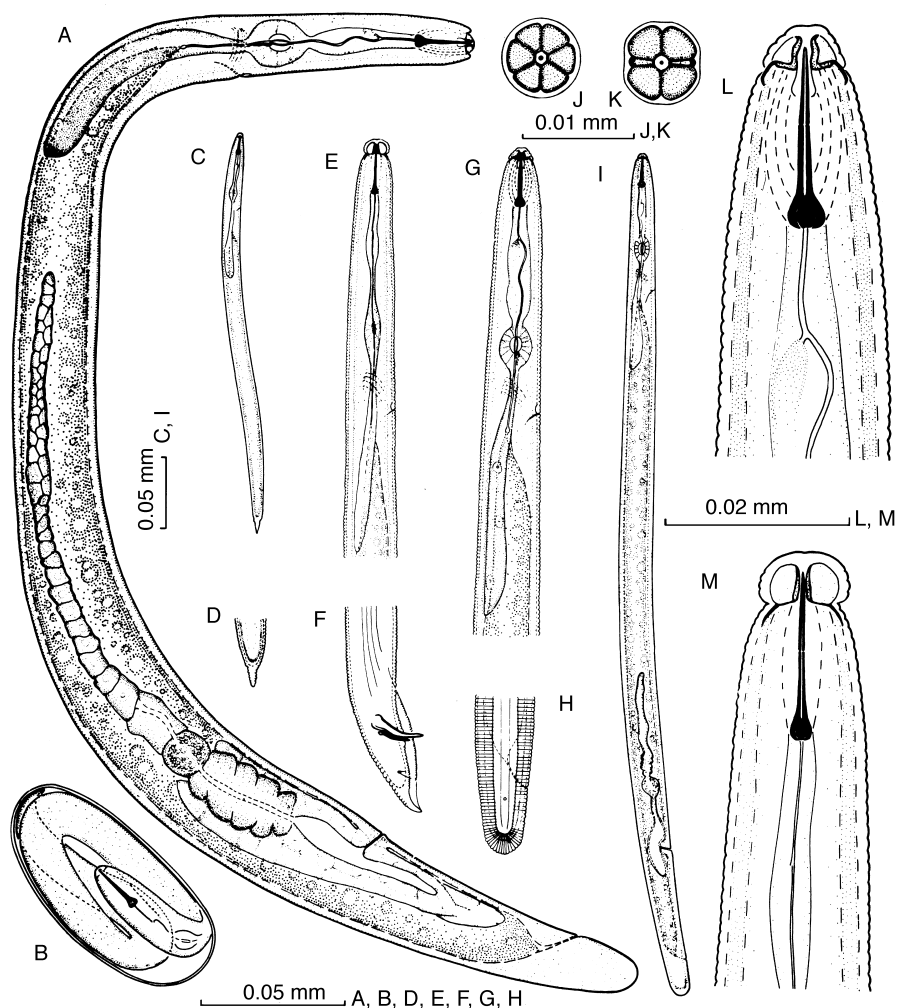


Fig. 72. *Acontylus vipriensis* Meagher. A. Mature female. B. Embryonated egg. C and D. Juvenile. E and F. Head and tail ends of male, respectively. G and H. Head and tail ends of female. I. Immature female. J and K. *En face* views of female and male, respectively. L. Head end of female. M. Head end of male. (After Meagher, 1976.)

**Ovary single**, outstretched, with oocytes in one to two rows. Female tail subcylindroid, 1–1.5 anal body widths long, terminus annulated. Testis outstretched, sperm small, rounded. Male tail elongate-conoid, with 10  $\mu\text{m}$  long hyaline portion. Bursa surrounding tail tip. Spicules about 20  $\mu\text{m}$  long and distinctly cephalated in type species. Gubernaculum half as long as spicules, protrusible. **Juveniles with pointed tail** bearing 10  $\mu\text{m}$  long hyaline portion, well-developed stylet and oesophagus as in female. **Eggs laid singly within a gelatinous matrix.**

### Type species

*Acontylus vipriensis* Meagher, 1968

No other species.

ETYMOLOGY. Greek *akontion* = javelin, dart, *tylos* = knob (refers to dart-like knobbed stylet).

*Acontylus vipriensis* feeds ectoparasitically on roots of *Eucalyptus* sp., *Acacia* sp. and grass in Australia. The female body swells to a lesser degree than that in *Rotylenchulus* or *Verutus*. The nematode lays eggs in a gelatinous matrix and forms colonies on the roots (Meagher, 1968, 1976).

## FAMILY PRATYLENCHIDAE (Migratory endoparasitic Hoplolaimoidea)

This family contains elongate-slender nematodes with a low-arched, strongly sclerotized, cephalic region generally with two to three annules, well-developed stylet usually not more than three head widths long, moderate-size tails and oesophageal glands overlapping intestine with the subventrals extending past the dorsal gland. Juveniles, females and the males in some groups (Pratylenchinae, Hirschmanniellinae), are capable of penetrating and feeding on internal root tissues.

Species of *Pratylenchus*, popularly known as root lesion or meadow nematodes, are worldwide in distribution. Some species, e.g. *P. brachyurus*, *P. coffeae*, *P. penetrans*, *P. zeae*, attack and damage several important crops. The damage to the root system is due both to the direct feeding and physical activities of the nematodes, and to their digestive and metabolic secretions. The injury is aggravated by the contamination of the feeding sites with microorganisms. Several species may interact with pathogenic fungi (e.g. *P. brachyurus* with *Rhizoctonia solani*), causing greater damage than by nematodes or fungi alone. Large populations of nematodes build up in roots (over 10,000 *Pratylenchus* per gram of root of *Vicia faba*) and once decay sets in, the nematodes migrate through roots or soil to parasitize fresh tissues.

*Pratylenchus brachyurus* is widely distributed in peanut-growing areas of the southern USA. It can build up high populations and cause damage to roots, pegs and shells of peanut. *Pratylenchus coffeae* is pathogenic to citrus and banana (Siddiqi, 1964a). It has been implicated in a decline of sunki orange (*Citrus sunki*) in Taiwan. In Florida, USA, it may become as pathogenic to citrus as *Radopholus similis*. Virulent and non-virulent races of *P. coffeae* were found on sweet potato cultivars in Japan and it was suggested that the *P. coffeae* complex involved more than one species (Mizukubo & Sano, 1997). *Pratylenchus scribneri* and *P. alleni* are common parasites of soybean in midwestern USA. *Pratylenchus goodeyi* is an important parasite of banana in many parts of highland East Africa, where it is considered indigenous. *Pratylenchus penetrans* is pathogenic to alfalfa, apple, carrot, celery, pea, peach, peanut, strawberry, etc. *Pratylenchus thornei* is a menace to wheat growing in several countries (Australia, India, Mexico, etc.). The nematodes penetrate the parenchyma, often migrate intracellularly and are mostly found in the cortex, where they form cavities in which they feed on adjoining cells and multiply. It seems that the endodermis acts as a barrier to nematodes penetrating the stele.



*Pratylenchus penetrans* fed ectoparasitically on root hairs of rape, oil radish, tobacco and potato. The feeding involved probing, cell penetration by the stylet, salivation and food ingestion. All stages were observed to feed on root hairs, but adults soon moved into the root to feed endoparasitically (Zunke, 1990).

Soil temperature is an important factor in the development of *Pratylenchus* spp. For example, *P. brachyurus* and *P. zeae* develop faster at 28–35°C than at 15–25°C, completing their life cycle in 35–40 days in maize roots (Graham, 1951). *Pratylenchus* spp. are easily cultured on root callus tissue. *Pratylenchus coffeae* and *R. similis* have been propagated on citrus-leaf callus (Inserra & O'Bannon, 1975). *Pratylenchus thornei* and *Merlinius brevidens* survived in a state of anhydrobiosis in a dry-season habitat after a wheat crop had been harvested and 95 and 100% of their population in dry field roots and soil, respectively, revived after rehydration (Tobar *et al.*, 1995).

Bisexual *Pratylenchus* spp. multiplying by amphimixis have low chromosome numbers, e.g. *P. penetrans*  $2n = 10$ , *P. vulnus*  $2n = 12$ , *P. coffeae*  $2n = 14$ . The parthenogenetically reproducing species appear to be polyploids, e.g. *P. neglectus*  $2n = 20$ , *P. zeae*  $2n = 21$ –26, *P. brachyurus*  $2n = 30$ –32, and to have evolved from the amphimictic bisexual species. The variation in chromosome numbers in bisexual species indicates that the genus is heterogeneous and that the basic chromosome number in this group is difficult to determine (Roman & Triantaphyllou, 1969).

*Zygotylenchus guevarai* is widely distributed in France, Greece, Italy, Spain, Turkey, Yugoslavia and occurs in Bulgaria, Czechoslovakia, Hungary, Pakistan, Poland, Tunisia and West Germany. The species was described almost simultaneously under three different names as *Pratylenchoides guevarai* by Tobar Jiménez (1963) from Spain, as *Zygotylenchus browni* by Siddiqi (1963) from Tunisia and as *Mesotylus gallicus* by de Guiran (1964) from France. Like *Pratylenchus* spp., *Z. guevarai* is a migratory endoparasite of roots and builds up large populations in the root cortex, where it forms cavities.

*Hirschmanniella* spp. are well adapted to aquatic life and parasitize paddy and several aquatic grasses. *Hirschmanniella oryzae*, *H. magna* and *H. mucronata* are widely distributed in rice fields in India. *Hirschmanniella imamuri*, *H. oryzae* and *H. spinicaudata* are injurious to rice. *Hirschmanniella imamuri* has one generation per year, while *H. oryzae* has two (Kuwahara & Iyatomi, 1970). *Hirschmanniella mexicana* parasitizes stems and leaves of an aquatic rootless plant, *Ceratophyllum demersum* (coontail), in Florida, USA. *Hirschmanniella marina* causes necrotic lesions and swelling and shortening of internodes of rhizomes of a marine plant, *Diplanthera wrightii* Aschers, at low tide in Florida, USA (Sher, 1968).

The females and juveniles of the subfamily Radopholinae are migratory endoparasites of roots but the males have a degenerate oesophagus and stylet and probably cannot feed. The cephalic region is different in the two sexes. The females have a low-arched, strongly sclerotized head but in the males it becomes secondarily high arched and poorly sclerotized. This change in the male is possibly the result of an adaptation to provide space for enlarged amphids and their apertures for chemotactic location of the females for fertilization, the only function left for the non-feeding males. It is very marked in *Radopholus* and *Radopholoides*, less marked in *Hoplotylus* and poorly marked in *Pratylenchoides* and *Apratylenchoides*. The occurrence of thin rod-like sperm in members of this subfamily is a unique feature among the entire order of Tylenchida.

*Radopholus* is indigenous to Australia, mostly as parasites of wild plants and forest trees; only one of the 22 valid nominal species, namely *R. nigeriensis*, was found indigenous outside Australia (Sher, 1968a). *Radopholus nigeriensis* has now been transferred to a new genus, *Zygradus*, by Siddiqi (1991).

Siddiqi & Hahn (1995) stated that, since the genomic variation within a species or genus is likely to be greatest at its centre of origin and because recently two more new species (*R. citri* and *R. bridgei*) have been described from Indonesia, Australasia is the centre of origin of the genus *Radopholus* and probably also its type species, *R. similis*. *Radopholus bridgei* Siddiqi & Hahn, 1995 was differentiated from *R. similis* by morphological characters and by RAPD analysis using polymerase chain reaction (see p. 77 and Siddiqi & Hahn, 1995).

*Radopholus similis* occurs throughout tropical and warm temperate regions but appears to have been dispersed by man on such important plantation crops as banana, sugarcane, citrus, tea and black pepper. A wide distribution of *R. williamsi* (now *Achlysiella williamsi*) on similar crops is also man-made. *Radopholus similis* is one of the most important and destructive root parasites. The nematode causes extensive damage to root cortical tissues by its feeding and physical and physiological activities. Cavities and furrows in the cortex are formed where nematodes live and multiply but contamination by microorganisms soon initiates decay and the nematodes migrate to new feeding sites and habitats. They are capable of wiping out entire plantations of banana in Central and South America, citrus in Florida, pepper in Indonesia and tea in Sri Lanka and are a menace to coconut in South Indian coastal regions. It is a major parasite of coconut, arecanut, black pepper and banana in South India.

The citrus race of *R. similis* is physiologically and genetically isolated from the banana race and the two represent sibling species. They are morphologically similar to each other, but differ in chromosome number ( $n = 5$  in the citrus race and 4 in the banana race), genetic variability in protein, host preference and behaviour. The citrus race, which causes 'spreading decline' of citrus in Florida, USA was named *Radopholus citrophilus* by Huettel *et al.* (1984). It was considered as a subspecies of *R. similis* by Siddiqi (1986). *Radopholus citrophilus* has vulval lips extend to three annules (vs. two annules in *R. similis*) (Fig. 76, E a, b) and three to seven papilla-like structures on the anterior lip of cloacal aperture (vs. none to two in *R. similis*) (Fig. 76, F a, b). In SEM (see Huettel & Yaegashi, 1988), the female labial disc is more rounded as compared to more hexagonal in *R. s. similis* and lateral lips do not completely terminate at the third annule as in *R. s. similis*. Submedian and lateral lips appear to be more fused than in *R. s. similis* and chromosome number generally is  $n = 5$  ( $n = 4$  in *R. s. similis*).

Kaplan *et al.* (1997) have demonstrated that *R. similis* and *R. citrophilus* are not reproductively isolated and that gene flow between them can take place. Hence *R. citrophilus* becomes a junior synonym of *R. similis*. I still feel that the two races of *R. similis* are distinct enough to be considered at subspecies level. *Radopholus s. citrophilus* produces citrus dieback symptoms, defoliation, small fruit and significant losses in fruit production. A 4 ha citrus grove planted with seedlings infested with *R. s. citrophilus* produced 62 boxes of citrus  $\text{ha}^{-1}$  (\$123  $\text{ha}^{-1}$ ), while a similar-sized grove planted with clean seedlings produced 1322 boxes  $\text{ha}^{-1}$  (\$2644  $\text{ha}^{-1}$ ) (O'Bannon, 1977).

*Pratylenchoides* is indigenous in the Palaearctic region. The presence of deirids in *Pratylenchoides* is puzzling. The genus could have had an ancestor in common with *Amplimerlinius* (Merliniinae). The shape of the cephalic region, the subcylindroid

female tail with abnormally thickened cuticle at the tip, the lateral field of either side joined terminally, a fixed gubernaculum, the occurrence of six incisures in the lateral fields and the oesophageal glands sometimes forming a pseudo-bulb support this view. It should be noted that, like *Amplimerlinius* spp., *Pratylenchoides laticauda* was found feeding ectoparasitically on roots of *Monarda mollis* L. and *Mentha piperita* L. (Braun & Loof, 1967). Perhaps *Pratylenchoides* represents a separate evolutionary line descending from an *Amplimerlinius*-like form (see Baldwin *et al.*, 1983).

*Hoplotylus femina*, *H. sjacobi*, *H. silvaticus* and *H. triversus* occur in Holland, New Zealand, USA and Japan, respectively. *Hoplotylus silvaticus* is interesting because it parasitizes roots of a forest fern, *Thelypteris noveboracensis* (L.) (Aspleniaceae), and further studies might prove *Hoplotylus* to be one of the more ancient plant parasites. *Radopholoides*, the other genus of this subfamily, has two nominal species, the type occurring on *Vanilla fragrans* (Salisb.) in north-east Malagasy and the other on fan palm (*Livistona* sp.), kangaroo grass and forest oak in Queensland, Australia. *Apratylenchoides belli* was found in soil around roots of shadscale (*Atriplex confertifolia*) in Utah, USA. *Apratylenchoides homoglans* was found parasitizing roots of chrysanthemum in Bangalore, South India (Siddiqi *et al.*, 1991).

The systematics of this group has improved progressively with the knowledge of the genera and those later assigned to it. Thorne (1949) established the subfamily Pratylenchinae for *Pratylenchus*, *Radopholus*, *Nacobbus* and *Rotylenchulus*, genera that are sometimes assigned to individual families. Chitwood in Chitwood & Chitwood (1950) at about the same time proposed Nacobbinae for the genera with saccate mature females, i.e. *Nacobbus* and *Rotylenchulus*. Siddiqi (1963) later elevated the Pratylenchinae to Pratylenchidae to include the two subfamilies, Pratylenchinae and Nacobbinae. In Pratylenchinae, he included *Pratylenchus*, *Hirschmanniella*, *Pratylenchoides*, *Radopholus* and his new genus *Zygotylenchus*. With present reckoning, these genera belong to three different subfamilies, Pratylenchinae, Hirschmanniellinae and Radopholinae. This 'inflation' in higher categories is worth keeping as it seems to reflect different evolutionary trends of nematodes invading a common niche, the plant root, both as a feeding area and habitat. The root endoparasitism, migratory as well as sedentary, in Hoplolaimoidea must have been a result of convergent evolution. From a practical point of view, recognition of these family groups will also help in deciding the proper systematic positions of future genera.

Pratylenchidae basically have subventral oesophageal glands in their normal position (ancestral character) although they are asymmetrical. The dorsal shift of these glands is a derived character of some phylogenetic significance. This type of elongated, undisplaced, subventral glands of Pratylenchidae, Rotylenchulidae and Rotylenchoidinae provides a clue for tracing the evolution of the most advanced of the root-parasitic Hoplolaimina, the Meloidogynidae and Heteroderidae.

The reduction of the posterior branch of the female reproductive system has occurred in Pratylenchinae as well as Radopholinae. The pseudo-monodelphic genera of the latter (*Radopholoides*, *Hoplotylus*, *Apratylenchoides*) can easily be differentiated from pseudo-monodelphic *Pratylenchus* by the manifestation of the sexual dimorphism in the anterior region and the dorsal overlap of the intestine by the oesophageal glands. The genus *Radopholoides* differs from *Radopholus* only in the reduction of the posterior branch of the female reproductive system. *Achlysiella* is a more advanced group than *Radopholus* in that the adult female body swells while

feeding on one site, eggs are laid in a gelatinous matrix and the juveniles moult to adult stage without feeding. *Apratylenchoides* can be derived from didelphic *Pratylenchoides* by the loss of the posterior ovary.

Parsimony analyses of nucleotides of the D3 expansion region of the 26S rDNA of *Pratylenchus* spp. showed that they represented a paraphyletic assemblage (Al-Banna *et al.*, 1997). It was apparent that the outgroup taxon *Hirschmanniella belli* shared a common ancestor with the clade that included *Pratylenchus vulnus* and *P. crenatus* and that *Nacobbis aberrans* and *Radopholus similis* shared a common ancestor with *P. coffeae*, *P. scribneri*, *P. brachyurus* and *P. hexincisus*, while *P. thornei*, *P. penetrans* and *P. minyus* (*P. neglectus*) branched from the main *Pratylenchus* clade with each sharing a common ancestor with the rest of the species in the tree.

### **Family Pratylenchidae Thorne, 1949 (Siddiqi, 1963)**

**syn. Nacobbidae Chitwood in Chitwood & Chitwood, 1950  
(Golden, 1971)**

**Radopholidae Allen & Sher, 1967 (Khan & Nanjappa, 1972)**

#### **Diagnosis**

Hoplolaimoidea. **Vermiform nematodes** (except *Nacobbis*). Cuticle prominently annulated. Lateral fields each with four to six incisures, very rarely areolated behind oesophagus. Deirids absent (except *Pratylenchoides*). Phasmids pore-like, on tail well behind anus, extending into bursa as pseudoribs except in *Hirschmanniella*. **Female:** Amphids pore-like, indistinct, near oral opening which is surrounded by six labial pits. **Cephalic region low**, anteriorly flattened to broadly rounded, annulated; framework strongly sclerotized; labial disc inconspicuous, dumb-bell-shaped (SEM) in *Pratylenchus*, *Radopholus* and *Achlysiella*, but indistinguishable in *Hirschmanniella* (cf. Figs 58, A; 59, E; 79, J). **Stylet strong, length not exceeding three cephalic region widths** (except in *Hirschmanniella*); conus about as long as posterior part; knobs large, rounded, usually closely applied to shaft. Orifice of dorsal gland close (usually 2–3 µm) to stylet base. Precorpus slender. Postcorpus strongly muscular, with prominent refractive thickenings. Isthmus short. Oesophago-intestinal junction indistinct, with a refringent valvula. **Oesophageal glands extending over intestine**; subventral glands asymmetrical, extending past the dorsal gland; three gland nuclei usually lying in tandem. Vulva a transverse slit, submedian to more posterior but not subterminal; lips not modified; lateral membranes absent. Vagina directed inward. Didelphic, amphidelphic or pseudo-mono-prodelphic. Ovaries outstretched; posterior ovary degenerate in pseudo-monodelphic forms. Spermatheca large, rounded, with small round or rod-like sperm when impregnated. **Tail conoid, sub-cylindrical to elongate-conoid, about twice or more anal body width long**, with round to pointed tip which may bear a mucro (*Hirschmanniella*), generally with inconspicuous hyaline terminal portion. **Male:** Stylet and oesophagus similar to those in female or reduced as in Radopholinae. Tail elongate-conoid, bursa terminal or subterminal. Testis single, outstretched, spermatocytes in one or two rows. Spicules similar, cephalated, arcuate, pointed with subterminal opening on dorsal or ventral side. Gubernaculum simple, fixed, or complex with telamon or titillae, protrusible. Hypoptygma present or absent. Juveniles resemble females in having similar anterior region and tail. **Obligate migratory endoparasites of roots.**

## Type subfamily

Pratylenchinae Thorne, 1949

## Other subfamilies

Hirschmanniellinae Fotedar & Handoo, 1978

Nacobbinae Chitwood in Chitwood & Chitwood, 1950

Radopholinae Allen & Sher, 1967

**Key to subfamilies of Pratylenchidae**

1. Oesophageal glands extending over intestine mostly ventrally and ventrolaterally; no marked sexual dimorphism in anterior region ..... 2  
     Oesophageal glands extending over intestine mostly dorsally and dorsolaterally; with marked sexual dimorphism in anterior region ..... 3
2. Tails similar between sexes; phasmids near terminus ..... **Hirschmanniellinae**  
     Tails dissimilar between sexes; phasmids not near terminus ..... **Pratylenchinae**
3. Mature female spindle-shaped or batatiform, with numerous eggs within body, gall-inciting ..... **Nacobbinae**  
     Mature female not spindle-shaped or batatiform, not with numerous eggs within body, not gall-inciting ..... **Radopholinae**

**Subfamily Pratylenchinae Thorne, 1949**

## Diagnosis

Pratylenchidae. **No marked sexual dimorphism in anterior region.** Small-sized (under 1 mm long). Lateral field with four to six incisures. Cephalic region low, usually flattened, with two to three annules. Stylet generally less than 20  $\mu\text{m}$  long. Oesophageal glands lobe-like, about three body widths or less long, **mostly on ventral side of intestine**. Intestine of regular width, lacking 'thorneian cells'. Ovaries paired or single. Female tail three anal body widths or less long, subcylindrical to conoid, lacking a mucro. Male tail conoid, arcuate, completely enveloped by a bursa. Phasmids near middle of tail. Spicules arcuate, cephalated, with subterminal pore usually on ventral side. **Gubernaculum fixed.** Hypoptygma generally present. Endoparasites of roots causing typical lesions, rarely attacking aquatic or marsh plants.

## Type genus

*Pratylenchus* Filipjev, 1936

## Other genus

*Zygotylenchus* Siddiqi, 1963

**Key to genera of Pratylenchinae**

1. One functional ovary ..... *Pratylenchus*  
     Two functional ovaries ..... *Zygotylenchus*

## Genus *Pratylenchus* Filipjev, 1936

(*Pratylenchus* Filipjev, 1934 = *nomen nudum*)

(Fig. 73)

### Diagnosis

*Pratylenchinae*. No marked sexual dimorphism in anterior region. Lateral fields each with four to six incisures, occasionally with oblique median markings. Deirids absent. **Phasmids near middle of tail**. Cephalic region low, flattened anteriorly or rarely rounded, continuous with body contour; sclerotization massive; labial disc inconspicuous, in SEM dumb-bell-shaped, with six labial pits around a minute oral aperture; amphidial apertures pore-like, near labial disc, indistinct. Stylet 20  $\mu\text{m}$  or less long, with round, anteriorly flat or indented basal knobs. Median bulb oval to round, very muscular. Oesophageal glands usually less than two body widths long, extending over intestine mostly ventrally. Vulva in posterior region (usually at 70–80%). **Pseudo-mono-prodelphic, with only anterior ovary functional**. Postvulval uterine sac present, with or without rudiments of posterior ovary. Spermatheca large, rounded, usually axial. Female tail subcylindrical to conoid, usually about two to three anal body widths long; terminus smooth or annulated, devoid of a process or mucro. Bursa enclosing tail terminus. **Spicules with subterminal pore on dorsal side**. **Gubernaculum simple, trough-like, fixed**.

### Type species

*Pratylenchus pratensis* (de Man, 1880) Filipjev, 1936

syn. *Tylenchus pratensis* de Man, 1880

*Anguillulina pratensis* (de Man) Goffart, 1929

*Pratylenchus helophilus* Seinhorst, 1959

*Pratylenchus irregularis* Loof, 1960

### Other species

*Pratylenchus acuticaudatus* Braasch & Decker, 1989

*P. agilis* Thorne & Malek, 1968

*P. allenii* Ferris, 1961

*P. allius* (Shahina & Maqbool, 1996) comb. n.

syn. *Radopholus allius* Shahina & Maqbool, 1996 (? = *Pratylenchus thornei*)

*P. andinus* Lordello, Zamith & Boock, 1961

*P. angulatus* Siddiqi, 1994

*P. artemisiae* Sheng & Chen, 1994

*P. australis* Valenzuela-A. & Raski, 1985 (syn. of *P. bolivianus* for Frederick & Tarjan, 1989)

*P. barkati* Das & Sultana, 1979 (sp. inq. for Loof, 1991)

*P. bhattii* Siddiqi, Dabur & Bajaj, 1991

*P. bolivianus* Corbett, 1983

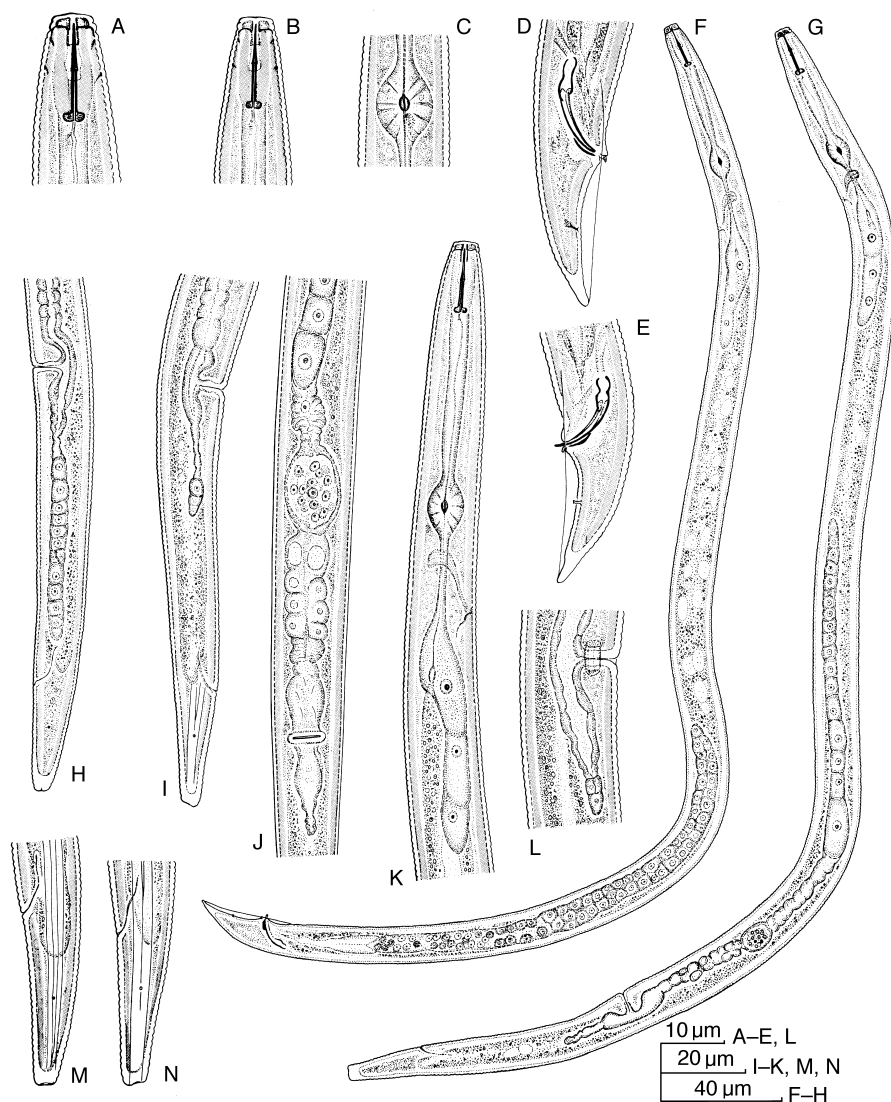
*P. brachyurus* (Godfrey, 1929) Filipjev & Schuurmans Stekhoven, 1941

syn. *Tylenchus brachyurus* Godfrey, 1929

*Anguillulina brachyurus* (Godfrey) Goodey, 1932

*Pratylenchus leioccephalus* Steiner, 1949

*Pratylenchus steineri* Lordello, Zamith & Boock, 1954



**Fig. 73.** *Pratylenchus coffeae* (Zimmermann). B–F Males, remainder females. A–G, I–L. Topotypes. H, M and N. From coffee soil, South India. A and B. Head ends. C. Median oesophageal bulb. D, E, H, I, M and N. Tail ends. F. Male. G. Female. J and L. Vulval regions. K. Oesophageal region. (After Siddiqi (1972): *CIH Descriptions of Plant-parasitic Nematodes*.)

*P. brassicae* (Shahina & Maqbool, 1996) comb. n.

syn. *Radopholus brassicae* Shahina & Maqbool, 1996 (= ? *P. coffeae*)

*P. cerealis* Haque, 1966 (sp. inq. for Loof, 1978, 1991; valid sp. for Handoo & Golden, 1989)

- P. chrysanthus* Edward, Misra, Rai & Peter, 1969 (sp. inq. for Loof, 1978, 1991 and Handoo & Golden, 1989)
- P. codiae* Singh & Jain, 1984 (sp. inq. for Loof, 1991)
- P. coffeae* (Zimmermann, 1898) Filipjev & Schuurmans Stekhoven, 1941 (Goodey, T., 1951, also proposed this combination)
- syn. *Tylenchus coffeae* Zimmermann, 1898
- Anguillulina coffeae* (Zimmermann) Goodey, 1932
- Tylenchus musicola* Cobb, 1919
- Anguillulina musicola* (Cobb) Goodey, 1932 (Goodey's species was renamed later as *P. goodeyi*)
- Pratylenchus musicola* (Cobb) Filipjev, 1936
- Tylenchus mahogani* Cobb, 1920
- Anguillulina mahogani* (Cobb) Goodey, 1932
- Pratylenchus mahogani* (Cobb) Filipjev, 1936
- P. conwallariae* Seinhorst, 1959
- P. crassi* Das & Sultana, 1979 (sp. inq. for Loof, 1991)
- P. crenatus* Loof, 1960
- syn. *P. pratensis* apud Thorne (1949)
- P. crossandrae* Subramaniam & Sivakumar, 1991
- P. cruciferus* Bajaj & Bhatti, 1984
- P. curvicauda* Siddiqi, Dabur & Bajaj, 1991
- P. dasi* Fortuner, 1985 (= nom. nov. for *P. capitatus* Das & Sultana, 1979; sp. inq. for Loof, 1991)
- syn. *Pratylenchus capitatus* Das & Sultana, 1979 (= primary homonym of *P. capitatus* Ivanova, 1968)
- Pratylenchus hyderabadensis* Singh & Gill, 1986 (= nom. nov. for *P. capitatus* Das & Sultana, 1979)
- Pratylenchus hyderabadensis* Singh & Gill, 1986 (= species name an unjustified amendment)
- P. delattrei* Luc, 1958
- syn. *Pratylenchus singhi* Das & Sultana, 1979
- Pratylenchus portulacis* Zarina & Maqbool, 1998
- P. dioscoreae* Yang & Zhao, 1992
- P. ekrami* Bajaj & Bhatti, 1984
- P. elamini* Zeidan & Geraert, 1991
- P. emarginatus* Eroshenko, 1978 (sp. inq. for Loof, 1991)
- P. estoniensis* Ryss, 1982
- P. exilis* Das & Sultana, 1979 (sp. inq. for Loof, 1991)
- P. fallax* Seinhorst, 1968 (syn. of *P. cerealis* for Frederick & Tarjan, 1989)
- P. flakkensis* Seinhorst, 1968
- P. gibbicaudatus* Minagawa, 1982
- P. globulicola* Romaniko, 1960 (syn. of *P. penetrans* for Loof, 1978, 1991)
- P. goodeyi* Sher & Allen, 1953
- syn. *Tylenchus musicola* apud Goodey, 1928
- P. gotohi* Mizukubo & Minagawa, 1991
- P. graminis* Subramaniam & Sivakumar, 1991
- P. hexincisus* Taylor & Jenkins, 1957



- P. japonicus* Ryss, 1988  
syn. *Pratylenchus macrostylus japonicus* Ryss, 1988 (Mizukubo *et al.* (1997) elevated it to species level)
- P. jordanensis* Hashim, 1984
- P. kasari* Ryss, 1982
- P. kralli* Ryss, 1982
- P. kumaoensis* Lal & Khan, 1990
- P. loofi* Singh & Jain, 1984 (sp. inq. for Loof, 1991)
- P. loosi* Loof, 1960  
syn. *Pratylenchus coffeae* apud Loos, 1953
- P. macrostylus* Wu, 1971
- P. manaliensis* Khan & Sharma, 1992
- P. manohari* Quraishi, 1982 (syn. of *P. cerealis* for Frederick & Tarjan, 1989; sp. inq. for Loof, 1991)
- P. mediterraneus* Corbett, 1983
- P. microstylus* Bajaj & Bhatti, 1984
- P. morettoii* Luc, Baldwin & Bell, 1986
- P. mulchandi* Nandakumar & Khera, 1970  
syn. *Pratylenchus muli* Nandakumar & Khera, 1969 (= nomen nudum)
- P. neglectus* (Rensch, 1924) Filipjev & Schuurmans Stekhoven, 1941  
syn. *Aphelenchus neglectus* Rensch, 1924  
*Tylenchus neglectus* (Rensch) Steiner, 1928  
*Anguillulina (Pratylenchus) neglecta* (Rensch) W. Schneider, 1939  
*Pratylenchus minyus* Sher & Allen, 1953  
*Pratylenchus capitatus* Ivanova, 1968  
*Pratylenchus neocapitatus* Khan & Singh, 1975  
*Pratylenchus similis* Khan & Singh, 1975
- P. neobrachyurus* Siddiqi, 1994
- P. nizamabadensis* Maharaju & Das, 1981 (sp. inq. for Loof, 1991)
- P. obtusicaudatus* Romaniko, 1977 (sp. inq. for Loof, 1991)
- P. okinawaensis* Minagawa, 1991
- P. panamaensis* Siddiqi, Dabur & Bajaj, 1991  
syn. *Pratylenchus gutierrezii* Golden, López Ch. & Vilchez R., 1992, syn. n.
- P. penetrans* (Cobb, 1917) Filipjev & Schuurmans Stekhoven, 1941  
syn. *Tylenchus penetrans* Cobb, 1917, male, nec female  
*Anguillulina (Pratylenchus) penetrans* (Cobb) Goodey, 1932  
*Tylenchus gulosus* Kühn, 1890 (= nomen oblitum)  
*Pratylenchus gulosus* (Kühn) Filipjev & Schuurmans Stekhoven, 1941
- P. pinguicaudatus* Corbett, 1969
- P. pratensisobrinus* Bernard, 1984 (syn. of *P. pratensis* for Frederick & Tarjan, 1989)
- P. pseudocoffeae* Mizukubo, 1992
- P. pseudofallax* Café Filho & Huang, 1989
- P. pseudopratensis* Seinhorst, 1968  
syn. *P. sefaensis* Fortuner, 1973
- P. ranjani* Khan & Singh, 1975 (sp. inq. for Loof, 1978; valid sp. for Handoo & Golden, 1989)  
(*Pratylenchus peelari* in Chawla & Prasad, 1973 = nomen nudum)

- P. roseus* Zarina & Maqbool, 1998  
*P. scribneri* Steiner in Sherbakoff & Stanley, 1943  
     syn. *Tylenchus penetrans* Cobb, 1917; female only  
*P. sensillatus* Anderson & Townshend, 1985  
*P. septincisus* Chang, 1991  
*P. stupidus* Romaniko, 1977 (sp. inq. for Loof, 1991)  
*P. subpenetrans* Taylor & Jenkins, 1957  
*P. subranjani* Mizukubo, Toida, Keereewan & Yoshida, 1990  
*P. sudanensis* Loof & Yassin, 1971  
*P. tenuis* Thorne & Malek, 1968 (sp. inq. for Loof, 1978, 1991, valid sp. for Handoo & Golden, 1989)  
*P. teres* Khan & Singh, 1975  
*P. thornei* Sher & Allen, 1953 (*P. thornei* Sher, 1948 = nom. nud.)  
*P. tulaganovi* Samibaeva, 1966 (sp. inq. for Loof, 1978, 1991)  
*P. typicus* Rashid, 1974  
*P. unzenensis* Mizukubo, 1992  
*P. uralensis* Romaniko, 1966 (sp. inq. for Loof, 1991)  
*P. variacaudatus* Romaniko, 1977 (sp. inq. for Loof, 1991)  
*P. ventroprojectus* Bernard, 1984 (syn. of *P. kralli* for Frederick & Tarjan, 1989)  
*P. vulnus* Allen & Jensen, 1951  
*P. wescolagricus* Corbett, 1984  
*P. yamagutii* Minagawa, 1991  
*P. yassini* Zeidan & Geraert, 1991  
*P. zae* Graham, 1951  
     syn. *Pratylenchus cubensis* Razjivin & O'Relly, 1976  
     (*P. zae* Steiner in Clayton & McMurtrey, 1950 = nomen nudum)  
*Pratylenchus impar* Khan & Singh

### Species inquirendae

- Pratylenchus bicaudatus* Meyl, 1954 (Meyl, 1961)  
     syn. *Pratylenchus pratensis bicaudatus* Meyl, 1954  
*P. brevicercus* Das, 1960  
*P. clavicaudatus* Baranovskaya & Haque, 1968  
*P. coffeae brasiliensis* Lordello, 1956 (? syn. of *P. zae*)  
*P. heterocercus* (Kreis, 1930) Andr  ssy, 1960  
     syn. *Dolichodorus heterocercus* Kreis, 1930 (syn. of *P. penetrans* for Andr  ssy, 1960)  
*P. indicus* Das, 1960  
*P. kolourus* Fortuner, 1985 (was a nom. nov.)  
     syn. *Tylenchus* (*Chitinotylenchus*) *coffeae brevicauda* Rahm, 1928  
*P. montanus* Zyubin, 1966  
*P. obtusus* (Bastian, 1865) Goodey, 1951  
     syn. *Tylenchus obtusus* Bastian, 1865  
         *Anguillulina obtusa* (Bastian) Goodey, 1932  
         *Rotylenchus obtusus* (Bastian) Filipjev, 1936  
         *Tylenchorhynchus obtusus* (Bastian) Filipjev & Schuurmans Stekhoven, 1941  
*P. pratensis tenuistriatus* Meyl, 1953  
*P. sacchari* (Soltwedel, 1888) Filipjev, 1936

syn. *Tylenchus sacchari* Soltwedel, 1888

*Anguillulina sacchari* (Soltwedel) Goodey, 1932

*P. tumidiceps* Merzheevskaya, 1951

#### Nomina nuda

*Pratylenchus angelicae* Kapoor, 1983

*P. himalayaensis* Kapoor, 1983

*P. menthae* Kapoor, 1983

*P. rhizasinus* Sher, 1948

ETYMOLOGY. Derived from first three letters of its type species name *pratensis*, and *Tylenchus*.

The type species was found in moist soil in a meadow near Leiden, The Netherlands (see Loof, 1960a, 1961). The latest keys to species of *Pratylenchus* are given by Frederick & Tarjan (1989), Handoo & Golden (1989) and Café Filho & Huang (1989).

#### Genus *Zygotylenchus* Siddiqi, 1963

syn. *Mesotylus* de Guiran, 1964

(Figs 8(b)B; 74, A–F)

#### Diagnosis

*Pratylenchinae*. Small-sized (less than 1 mm). No marked sexual dimorphism in anterior region. Lateral field with four incisures, not areolated. **Deirids absent**. Phasmids near middle of tail. Cephalic region low, slightly tapering, anteriorly truncate or rounded, continuous, annulated; framework strongly sclerotized, outer margins conspicuously extending into body, vestibulum extension tubular. Stylet strong, with round basal knobs. Postcorpus rounded. Isthmus short. **Oesophageal glands extending over intestine mostly ventrally, subventral glands asymmetrical**; oesophago-intestinal junction indistinct, ventral to main body of glands, about one body width behind median bulb, anterior to gland nuclei. Vulva slightly posterior to middle. Didelphic. **Ovaries paired**, outstretched, rarely tip of one of the ovaries reflexed. Oocytes in a row. Spermathecae round, with small round sperm when impregnated. Female tail cylindrical or slightly tapering, with smooth, more or less rounded terminus, two to three anal body widths long. Male tail tapering to a pointed terminus, completely enveloped by a bursa. Spicules cephalated, arcuate, **with subterminal pore on ventral side**, 18–21  $\mu\text{m}$  long in type species. Gubernaculum small, trough-shaped, fixed.

#### Type species

*Zygotylenchus browni* Siddiqi, 1963

#### Present status

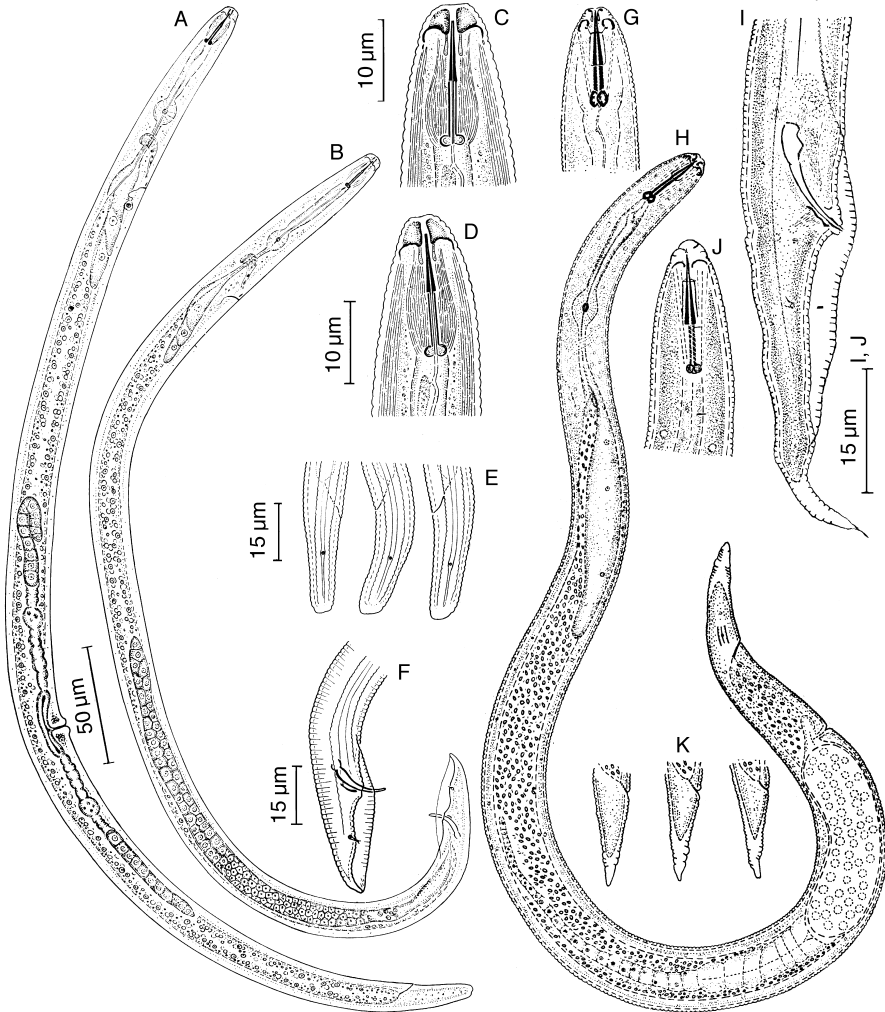
*Zygotylenchus guevarai* (Tobar Jiménez, 1963) Braun & Loof, 1966

syn. *Pratylenchoides guevarai* Tobar Jiménez, 1963

*Zygotylenchus browni* Siddiqi, 1963

*Mesotylus gallicus* de Guiran, 1964

*Zygotylenchus gallicus* (de Guiran) Braun & Loof, 1966



**Fig. 74.** A–F. *Zygotylenchus guevarai* (Tobar Jiménez) (= *Z. browni* Siddiqi). G–K. *Hoplotylus femina* s'Jacob. A and H. Females. B. Male. C and G. Head ends of females. D and J. Head ends of males. E and K. Female tails. F and I. Male tails. (A–F. After Siddiqi (1963), courtesy Springer-Verlag, Heidelberg. G–K. After s'Jacob (1960, 1979), courtesy Nematologica.)

#### Other species

*Zygotylenchus taomasinae* (de Guiran, 1964) Braun & Loof, 1966

syn. *Mesotylus taomasinae* de Guiran, 1964

*Pratylenchoides taomasinae* (de Guiran) Tarjan & Weischer, 1965

#### Species incerta sedis

*Zygotylenchus biterminalis* Razjivin & Milan, 1978

ETYMOLOGY. From Greek *zygos* = yoke, joining together (of *Pratylenchus* and *Radopholus*), and *Tylenchus*.

The type species was collected from soil and roots of *Capsicum annuum* L. in Tunisia.

## Subfamily Hirschmanniellinae Fotedar & Handoo, 1978

### Diagnosis

Pratylenchidae. **Moderate to large** (1–4 mm) and **slender** (a = usually 50–70). **No marked sexual dimorphism in anterior region**. Cuticle finely annulated. Lateral fields each with four incisures, reducing towards extremities. Cephalic region continuous, usually hemispheroidal, framework strongly sclerotized. Face view smooth; no differentiation of lip areas or oral disc. Stylet large. **Oesophageal glands elongated, overlapping intestine mostly ventrally**. Didelphic, amphidelphic. **Tails elongate-conoid, with a terminal mucro, similar between sexes**. Bursa large, subterminal. Spicules with subterminal pore on dorsal side. Gubernaculum simple, fixed. **Phasmids in posterior third of tail**. Endoparasites of roots mostly of aquatic plants.

### Type genus

*Hirschmanniella* Luc & Goodey, 1964

No other genus.

### Genus *Hirschmanniella* Luc & Goodey, 1964

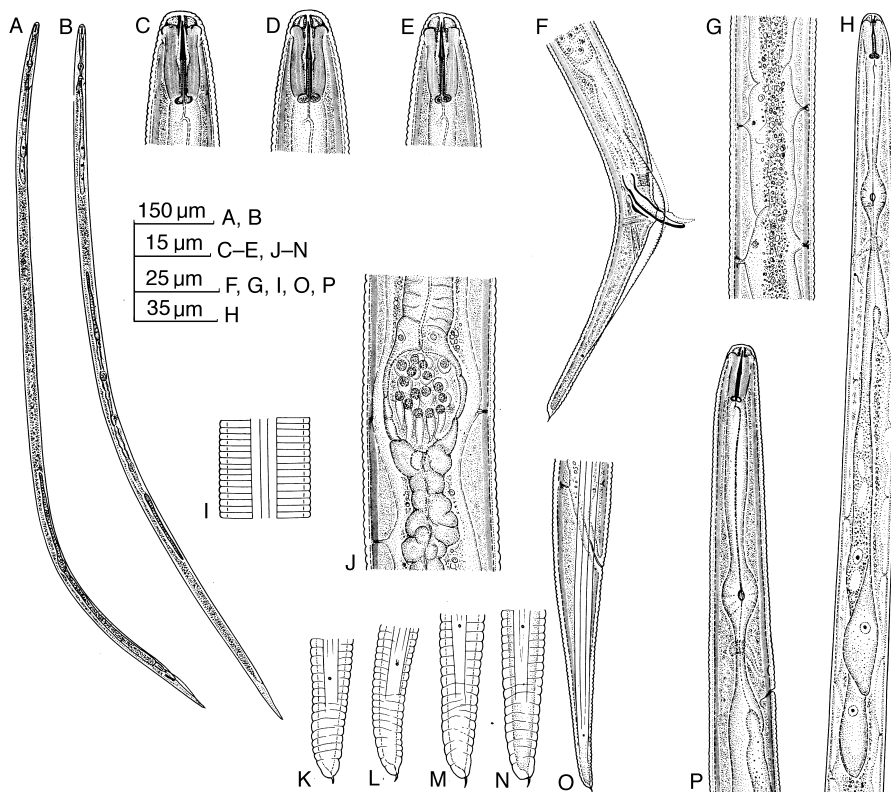
syn. *Hirschmannia* Luc & Goodey, 1962

nec *Hirschmannia* Eloffson, 1941 (Crustacea)

(Figs 58, A & B; 75)

### Diagnosis

Hirschmanniellinae. Long and slender nematodes (L = 1–4 mm; a = 40–79), straight to arcuate upon relaxation. Lateral field with four incisures, areolated towards extremities. Deirids absent. **Phasmids** pore-like, **near tail tip**. Amphid apertures labial, **transverse oval slit-like**. Cephalic region continuous, anteriorly flattened or hemispherical; framework heavily sclerotized, labial disc indistinct; annules not divided into sectors. Stylet massive, 15–46  $\mu\text{m}$ , usually three to five times maximum width of cephalic region; conus tubular; basal knobs large, rounded, close to shaft. Orifice of dorsal gland close to stylet base. Median oesophageal bulb round to oval, slightly offset from precorpus, with distinct refractive thickenings. Oesophageal glands elongated, lying ventral to intestine; **subventral glands asymmetrical, larger and much longer than the dorsal gland, nuclei of the three glands lying in a row, well separated from each other**. Excretory pore near oesophago-intestinal junction, behind hemizonid. Intestine with refractive food globules, may extend over rectum into tail; ‘thorneian cells’, a connective tissue-like formation with accumulated glycogen, present between intestine and muscle layer of body-wall. Vulva transverse, lips not modified. **Two branches of female reproductive organs equally developed** and outstretched in opposite directions. Spermathecae round to oval, axial. Ovaries mostly with single row of oocytes. Male with outstretched testis. Spicules with subterminal pore appearing to be on dorsal side. Gubernaculum fixed. **Tails similar**



**Fig. 75.** *Hirschmanniella oryzae* (van Breda de Haan), topotypes. A, E, F and P. Males, remainder females. A. Male. B. Female. C–E. Head ends. F and K–O. Tail ends. G. Midbody region showing 'thorneian cells' joining hypodermis and intestine. H. Oesophageal region. I. Lateral field at midbody. J. Spermatheca with sperm. P. Oesophageal region. (After Siddiqi, 1973.)

**between sexes**, elongate-conoid, usually with a terminal mucro; male tail carrying a simple, crenate, subterminal **bursa lacking phasmidial pseudoribs**. Cloacal lips not modified; hypopygium absent.

#### Type species

- Hirschmanniella spinicaudata* (Schuurmans Stekhoven, 1944) Luc & Goodey, 1964  
 syn. *Tylenchorhynchus spinicaudatus* Schuurmans Stekhoven, 1944  
*Hirschmannia spinicaudata* (Schuurmans Stekhoven) Luc & Goodey, 1962  
*Radopholus lavabri* Luc, 1957  
*Hirschmanniella lavabri* (Luc) Sher, 1968

## Other species

- Hirschmanniella abnormalis* Renubala, Dhanachand & Gambhir, 1992 (syn. of *H. loofi* for Loof, 1991)
- H. anchoryzae* Ebsary & Anderson, 1982
- H. areolata* Ebsary & Anderson, 1982
- H. asteromucronata* Razjivin, Fernandez, Ortega & Quincosa, 1981
- H. behningi* (Micoletzky, 1923) Luc & Goodey, 1964  
syn. *Tylenchorhynchus behningi* Micoletzky, 1923  
*Anguillulina* (*Tylenchorhynchus*) *behningi* (Micoletzky) W. Schneider, 1939  
*Hirschmannia behningi* (Micoletzky) Luc & Goodey, 1962  
*Radopholus behningi* (Micoletzky) Allen, 1955
- H. belli* Sher, 1968
- H. brassicae* Duan, Liu, Liu, Zhao (*et al.*), 1996
- H. caribbeana* Van den Berg & Quénéhervé, 2000
- H. caudacrena* Sher, 1968 (syn. of *H. mexicana* for Luc, 1987)
- H. diversa* Sher, 1968
- H. exacta* Kakar, Siddiqui & Khan, 1994
- H. furcata* Razjivin, Fernandez, Ortega & Quincosa, 1981
- H. gracilis* (de Man, 1880) Luc & Goodey, 1964  
syn. *Tylenchus gracilis* de Man, 1880  
*Tylenchorhynchus gracilis* (de Man) Micoletzky, 1925  
*Anguillulina gracilis* (de Man) Goodey, 1932  
*Chitinotylenchus gracilis* (de Man) Hirschmann, 1955  
*Radopholus gracilis* (de Man) Allen, 1955 (also n. comb. by Hirschmann, 1955)  
*Hirschmannia gracilis* (de Man) Luc & Goodey, 1962  
*Radopholus gigas* Andrásy, 1954  
*Hirschmanniella gigas* (Andrásy) Sher, 1968
- H. imamuri* Sher, 1968  
syn. *Tylenchus gracilis* apud Imamura, 1931
- H. kaverii* Sivakumar & Khan, 1982 (probably syn. of *H. mucronata*)
- H. loofi* Sher, 1968
- H. magna* Siddiqui, 1966  
syn. *Hirschmanniella dubia* Khan, 1972
- H. marina* Sher, 1968
- H. mexicana* (Chitwood, 1951) Sher, 1968  
syn. *Halenchus mexicanus* Chitwood, 1951
- H. microtyla* Sher, 1968
- H. miticausa* Bridge, Mortimer & Jackson, 1984
- H. mucronata* (Das, 1960) Khan, Siddiqui, Khan, Husain & Saxena, 1964  
syn. *Radopholus mucronatus* Das, 1960  
*Hirschmanniella mucronata* (Das) Timm, 1965  
*H. mucronata* (Das) Luc & Goodey, 1963 in Sher, 1968  
*H. mangalorensis* Mathur & Prasad, 1971  
*H. indica* Ahmad, 1974 (see redescription of *H. mucronata* in Khan, 1972)
- H. nghetinhensis* Eroshenko & Chau in Eroshenko, Tyau, Tkhan & Kan, 1985
- H. obesa* Razjivin, Fernandez, Ortega & Quincosa, 1981

- H. ornata* Eroshenko & Chau in Eroshenko, Tyau, Tkhan & Kan, 1985  
*H. orycrena* Sultana, 1979  
*H. oryzae* (van Breda de Haan, 1902) Luc & Goodey, 1964  
   syn. *Tylenchus oryzae* van Breda de Haan, 1902  
     *Anguillulina oryzae* (van Breda de Haan) Goodey, 1932  
     *Hirschmannia oryzae* (van Breda de Haan) Luc & Goodey, 1962  
     *Radopholus oryzae* (van Breda de Haan) Thorne, 1949  
     *Rotylenchus oryzae* (van Breda de Haan) Filipjev & Schuurmans Stekhoven, 1941  
     *Tylenchus apapillatus* Imamura, 1931  
     *Anguillulina apapillata* (Imamura) Goodey, 1932  
     *Rotylenchus apapillatus* (Imamura) Filipjev, 1936  
     *Hirschmanniella apapillata* (Imamura) Siddiqi, 1986  
     *Hirschmanniella nana* Siddiqi, 1966  
     *Hirschmanniella exigua* Khan, 1972  
*H. pisquidensis* Ebsary & Pharoah, 1982  
*H. pomponiensis* Abdel-Rahman & Maggenti, 1987 (nom. nud. in Abdel-Rahman, 1981)  
*H. shamimi* Ahmad, 1974  
*H. thornei* Sher, 1968  
*H. truncata* Razjivin, Fernandez, Ortega & Quincosa, 1981  
*H. zostericola* (Allgén, 1934) Luc & Goodey, 1964  
   syn. *Tylenchus* (*Chitinotylenchus*) *zostericola* Allgén, 1934  
     *Halenchus zostericola* (Allgén) Chitwood, 1951  
     *Radopholus zostericola* (Allgén) Allen, 1955  
     *Hirschmannia zostericola* (Allgén) Luc & Goodey, 1962

#### Species inquirenda

- Hirschmanniella minor* (Goffart, 1933) Siddiqi, 1986  
   syn. *Anguillulina gracilis* var. *minor* Goffart, 1933

#### Nomina nuda

- Hirschmanniella augusta* Kapoor, 1983  
*H. oryzae* (Soltwedel, 1889) Luc & Goodey in Sher, 1968  
   syn. *Tylenchus oryzae* Soltwedel, 1889  
*H. phantastica* Kapoor, 1983  
*H. pomponiensis* Abdel-Rahman, 1981

ETYMOLOGY. Patronym honouring Hedwig Hirschmann.

The type species was found in fresh water, Vitsumbi Bay, Lake Edouard, Zaïre, Africa.

#### Note

Face views (SEM) of *Hirschmanniella* spp. are somewhat similar to those of *Amplimerlinius* and *Helicotylenchus* spp.



## Subfamily Radopholinae Allen & Sher, 1967

syn. *Hoplotylinae* Khan, 1969 (also proposed by Siddiqi, 1971)

### Diagnosis

Pratylenchidae. Small to medium-sized (about 1 mm or less long), **vermiform**. **Sexual dimorphism in cephalic region, stylet and oesophagus present**. Cuticle distinctly annulated. Lateral fields each with three to seven incisures, usually not areolated. Deirids absent except in *Pratylenchoides*. Cephalic region of juveniles and females low, hemispherical or slightly conoid, continuous or offset; framework strongly sclerotized, in male high arched and often offset, with reduced sclerotization; labial disc indistinct. Stylet well developed in juveniles and females, about two to three times cephalic region width long, in males generally reduced, may be rudimentary. **Oesophageal glands overlapping intestine mostly dorsally and dorsolaterally**. Didelphic, amphidelphic or with posterior branch reduced or represented by a uterine sac. **Tails usually over twice anal body width long, often with distinct hyaline terminal portion**. Female tail variable, elongate-conoid to cylindroid: male tail elongate-tapering, similar or dissimilar to that of female. Bursa subterminal or terminal, with phasmidial pseudoribs. Phasmids near middle of tail or more anterior. **Spicules with subterminal pore on ventral side**. **Gubernaculum protrusible, with titillae**, or fixed, without titillae. Migratory endoparasites of roots, sometimes sedentary and with slightly swollen mature females.

### Type genus

*Radopholus* Thorne, 1949

### Other genera

*Achlysiella* Hunt, Bridge & Machon, 1989

*Apratylenchoides* Sher, 1973

*Hoplotylus* s'Jacob, 1960

*Pratylenchoides* Winslow, 1958

*Radopholoides* de Guiran, 1967

*Zygradus* Siddiqi, 1991

### Key to genera of Radopholinae

1. Deirids present; at least one oesophageal gland nucleus opposite or anterior to oesophago-intestinal junction ..... *Pratylenchoides*  
Deirids absent; all oesophageal gland nuclei behind oesophago-intestinal junction ..... 2
2. Sexual dimorphism in anterior region prominent ..... 3  
Sexual dimorphism in anterior region not prominent ..... 6
3. Posterior ovary normally developed, functional ..... 4  
Posterior ovary reduced or absent, non-functional ..... 5
4. Mature female swollen to become sausage-shaped; juveniles moulting to adult stage without feeding ..... *Achlysiella*  
Mature female not swollen; juveniles moulting to adult stage with feeding ..... *Radopholus*

5. Female stylet 21–29  $\mu\text{m}$  long, basal knobs tulip-shaped ..... *Hoplotylus*  
     Female stylet under 20  $\mu\text{m}$  long, basal knobs not tulip-shaped ..... *Radopholoides*
6. Posterior ovary normally developed, functional ..... *Zygradus*  
     Posterior ovary reduced, non-functional ..... *Apratylenchoides*

## Genus *Radopholus* Thorne, 1949

syn. *Neoradopholus* Khan & Shakil, 1973

(Figs 59, E; 76, A, B, E and F)

### Diagnosis

Radopholinae. Sexual dimorphism in anterior region well marked, males having higher rounded and more offset cephalic region and cephalic framework, stylet and oesophagus markedly reduced. In SEM, female head shows submedian lips completely fused together and with labial disc and lateral lips extending to base of head. Body 0.4–0.9 mm long, not very slender ( $a$  = usually 20–30), straight to arcuate upon relaxation. Lateral fields each with three to seven incisures, not areolated. **Deirids absent.** Phasmids usually in anterior region of tail. Cephalic region in female low, continuous or slightly offset, annulated or smooth; framework strongly sclerotized. Stylet well developed in juveniles and females, conus about as long as shaft. Oesophageal glands elongated, mostly dorsal to intestine, subventral glands symmetrical or asymmetrical, much longer than the dorsal gland; **nuclei of the three glands lie behind oesophago-intestinal junction, sometimes in a row.** Excretory pore near oesophago-intestinal junction, just behind hemizonid. Vulva at 50–70% of body length (usually about 55–65%). Didelphic, amphidelphic. Spermathecae round to oval, axial, **in most species with rod-like**, rarely round, **sperm.** **Female tail elongate-conoid** to subcylindroid, usually two to four times anal body width long. Male tail generally more tapering than that of female; bursa subterminal or rarely terminal. Spicules cephalated, slightly arcuate. **Gubernaculum large, protrusible**, with or without distal titillae. Endoparasites of roots, native to Australian region; only one species, *R. similis*, has a worldwide distribution.

### Type species

*Radopholus similis* (Cobb, 1893) Thorne, 1949

syn. *Tylenchus similis* Cobb, 1893

*Anguillulina similis* (Cobb) Goodey, 1932

*Rotylenchus similis* (Cobb) Filipjev, 1936

*Tylenchus granulosus* Cobb, 1893 ( = senior synonym)

*Anguillulina granulosa* (Cobb) Goodey, 1932

*Tetylenchus granulosus* (Cobb) Filipjev, 1936

*Radopholus granulosus* (Cobb) Siddiqi, 1986

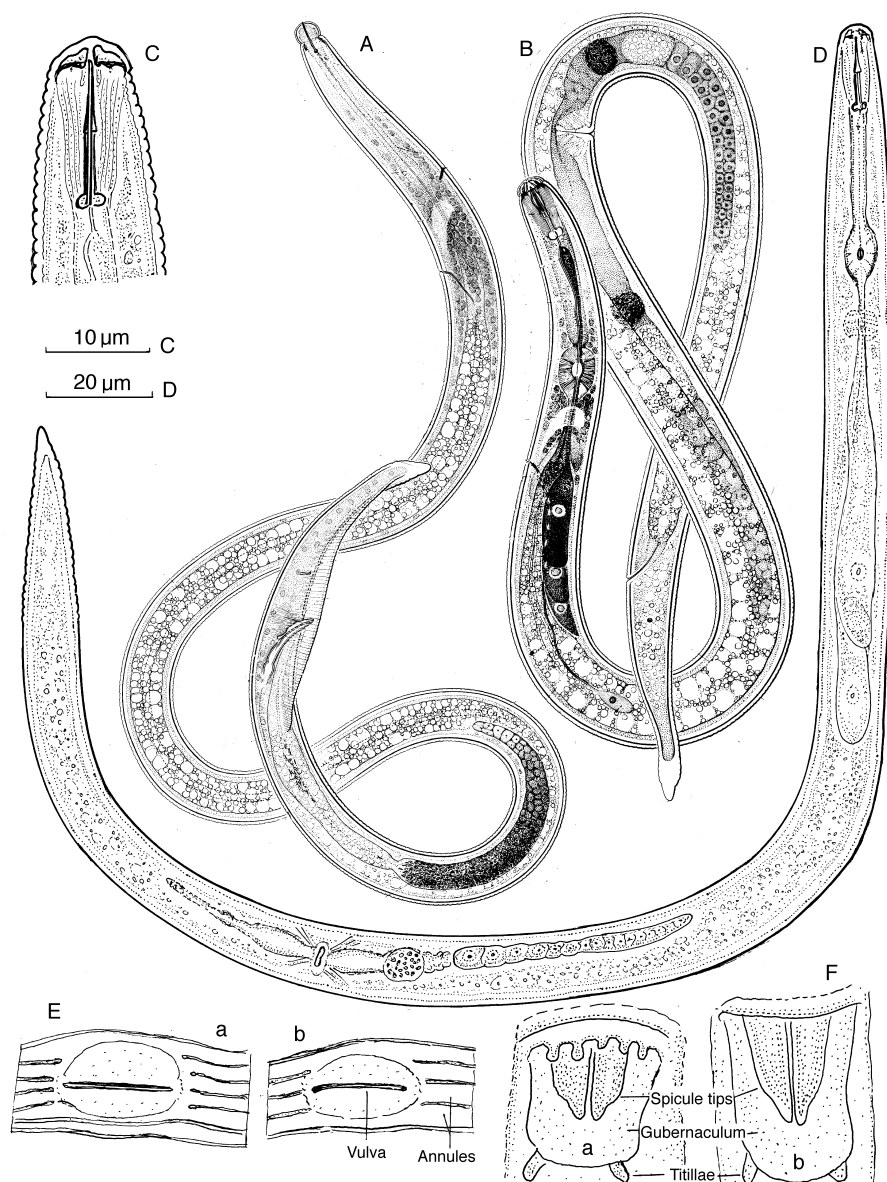
*Tylenchus acutocaudatus* Zimmermann, 1898

*Anguillulina acutocaudata* (Zimmermann) Goodey, 1932

*Tylenchorhynchus acutocaudatus* (Zimmermann) Filipjev, 1934

*Radopholus acutocaudatus* (Zimmermann) Siddiqi, 1986

*Tylenchus bififormis* Cobb, 1909



**Fig. 76.** A, B, E and F. *Radopholus similis* (Cobb). C and D. *Radopholoides litoralis* de Guiran, paratype. A. Male. B and D. Females. C. Head end of female. E. Vulva in ventral view, a, *R. similis citrophilus*, b, *R. similis similis*. F. Cloacal region in ventral view, a, *R. similis citrophilus*, b, *R. similis similis* (A and B. After Cobb (1915), courtesy US Department of Agriculture.)

*Anguillulina biformis* (Cobb) Goodey, 1932  
*Radopholus biformis* (Cobb) Siddiqi, 1986  
*Radopholus similis similis* Cobb, 1893 (Siddiqi, 1986)  
*Radopholus citrophilus* Huettel, Dickson & Kaplan, 1984  
*Radopholus similis citrophilus* Huettel, Dickson & Kaplan, 1984 (Siddiqi, 1986)

#### Subspecies of type species

*Radopholus similis similis* (Cobb, 1893) Thorne, 1949 (Siddiqi, 1986)  
*Radopholus similis citrophilus* Huettel, Dickson & Kaplan, 1984 (Siddiqi, 1986)  
 (= citrus race of *R. similis*)

#### Other species

*Radopholus bridgei* Siddiqi & Hahn, 1995  
*R. cavenessi* Egunjobi, 1968 (sp. inq. for Ryss & Wouts, 1997)  
*R. citri* Machon & Bridge, 1996  
*R. clarus* Colbran, 1971  
*R. crenatus* Colbran, 1971  
*R. inaequalis* Sauer, 1958  
 syn. *Neoradopholus inaequalis* (Sauer) Khan & Shakil, 1973  
*R. inanis* Colbran, 1971  
*R. intermedius* Colbran, 1971  
*R. kahikateae* Ryss & Wouts, 1997  
*R. megadorus* Colbran, 1971  
*R. nativus* Sher, 1968  
 syn. *Radopholus ferax* Colbran, 1971 (syn. for Ryss & Wouts, 1997)  
*R. nelsonensis* Ryss & Wouts, 1997  
*R. neosimilis* Sauer, 1958  
 syn. *Neoradopholus neosimilis* (Sauer) Khan & Shakil, 1973  
*R. rectus* Colbran, 1971  
*R. rotundisemenus* Sher, 1968  
*R. sanoi* Mizukubo, 1989  
*R. serratus* Colbran, 1971  
*R. vangundyi* Sher, 1968  
*R. vertexplanus* Sher, 1968

#### Remarks

*Tylenchus similis* Cobb and *Tylenchus granulosus* Cobb are congeneric and their descriptions appeared in the same publication. The former was based on the male, the latter on the female. The description of *T. granulosus* appeared first and thus this name has priority over *T. similis*. Article 24(a) and (b) of ICZN provides that the relative priority of taxa published simultaneously is determined by the action of the first reviser who believes them to represent the same taxonomic unit and that the reviser must have chosen one as the name of the taxon. These requirements were fulfilled by the action of Sher (1968a) who considered *T. similis* (= *Radopholus similis*) as the valid name and *T. granulosus* as nomen oblitum (forgotten name), which cannot be used now unless the International Commission on Zoological

Nomenclature so directs. Khan & Shakil (1973) proposed *Neoradopholus* with *R. inaequalis* as its type species, based on the character of the bursa enveloping the entire tail. This is not considered here sufficient to distinguish it from *Radopholus*.

Shahina & Maqbool (1996) described two new species of *Radopholus*, *R. allius* and *R. brassicae*, which had one functional ovary. No males were described. I examined the paratypes of the two species and found them to belong to the genus *Pratylenchus*, to which they are transferred here. The specimens were mounted with the anterior region slightly twisted so that the glands appeared to lie dorsal to the intestine.

ETYMOLOGY. From the Latin *radix* = root, and the Greek *philéin* = to love.

The type species was found around roots of diseased banana plants, (*Musa* sp. var. Dwarf Cavendish), Viti Levu Island, Fiji (Cobb, 1893). Ryss and Wouts (1997) described two new and two known species of *Radopholus* from native vegetation in New Zealand and gave a key to all the species of the genus.

### Genus *Radopholoides* de Guiran, 1967

(Fig. 76, C & D)

#### Diagnosis

Radopholinae. Sexual dimorphism in anterior region well marked. Small-sized (0.3–0.5 mm). Lateral field with four incisures. Cephalic region in females low, continuous round, annulated, framework heavily sclerotized; **in males high and round, knob-like** with slight sclerotization. Stylet 12–17  $\mu\text{m}$  long, **knobs round**, not fully adpressed to shaft. Oesophageal glands dorsal to intestine, two to three times body width long, nuclei in a row. Vulva posterior, at 66–72%. **Posterior ovary degenerate, non-functional**. Female tail three to four anal body widths long, tapering to a small round terminus, with or without striae around it, hyaline portion small, less than one-fourth of tail. Phasmids in anterior region of tail. **Bursa enclosing tail tip**. Spicules cephalated, almost straight, pointed. Gubernaculum about half spicule length, protrusible. Cloacal lips raised, rounded.

#### Type species

*Radopholoides litoralis* de Guiran, 1967

syn. *Radopholus litoralis* (de Guiran) Luc, 1987

#### Other species

*Radopholoides laevis* Colbran, 1971

syn. *Radopholus laevis* (Colbran) Luc, 1987

#### Species incerta sedis:

*Radopholoides scrijabini* Nesterov & Kozhokaru, 1980

#### Remarks

*Radopholoides* is very similar to *Radopholus*, differing in the rudimentation of the posterior branch of the female reproductive organs. Colbran (1971) noted that *Radopholoides laevis* was related phylogenetically to *Radopholus intermedius*, which

also shows a reduction in the development of the posterior branch of the female reproductive organs; both species are found in soil around roots of kangaroo grass in Australia. Luc (1987) placed *Radopholoides scrijabini* in *species incertae sedis* and commented that it was doubtful if it was a pratylenchid.

ETYMOLOGY. From *Radopholus*, and Greek *eidos* = likeness, similar.

The type species was found in soil around roots of *Vanilla fragrans* (Salisb.) and various grasses in Mandenya, Malagasy.

### Genus *Pratylenchoides* Winslow, 1958

syn. *Hoplorhynchus* Andr  ssy, 1985

(Fig. 77, A–E)

#### Diagnosis

Radopholinae. Small-sized (female 0.5–0.9 mm), straight to arcuate upon relaxation. Sexual dimorphism in anterior region present, with male head slightly raised and stylet and oesophagus less developed than in female. Annulations fine to moderately coarse. Lateral fields each with six or sometimes with four incisures. **Deirids distinct**. Cephalic region low, continuous, hemispherical to anteriorly flattened, annulated. In SEM, female head shows submedian lips fused with labial disc but six lip sectors remaining distinct from each other. Stylet 16–24 µm long in females, 15–23 µm in males; basal knobs rounded. Orifice of dorsal gland close to base of stylet. Oesophageal glands forming short to long overlap, mostly on dorsal side of intestine; **dorsal gland nucleus** and, in several species, one of the subventral gland nuclei **lying opposite or just anterior to oesophago-intestinal junction** which has a small oval valvula. Didelphic, amphidelphic. Spermathecae round, axial, **with round sperm**, which may rarely be rod-like (*P. bacilisemenus*). Ovaries outstretched. **Female tail subcylindroid**, with annulated terminus, rarely pointed with conspicuous hyaline portion (e.g. *P. maritimus*). Phasmids pore-like, generally in posterior region of tail, extending into bursa. Male tail subcylindrical anteriorly, then tapering to a conical, hyaline tip, more than twice anal body width long, completely enclosed in a simple crenate bursa. Cloacal lips slightly raised. Spicules prominently cephalated, arcuate, pointed. **Gubernaculum small, non-protrusible**. Migratory endoparasites of roots.

#### Type species

*Pratylenchoides crenicauda* Winslow, 1958

syn. *Anguillulina obtusa* of Goodey, 1932 & 1940

*Rotylenchus obtusus* of Filipjev & Schuurmans Stekhoven, 1941

*Pratylenchoides maqsoodi* Maqbool & Shahina, 1989, syn. n.

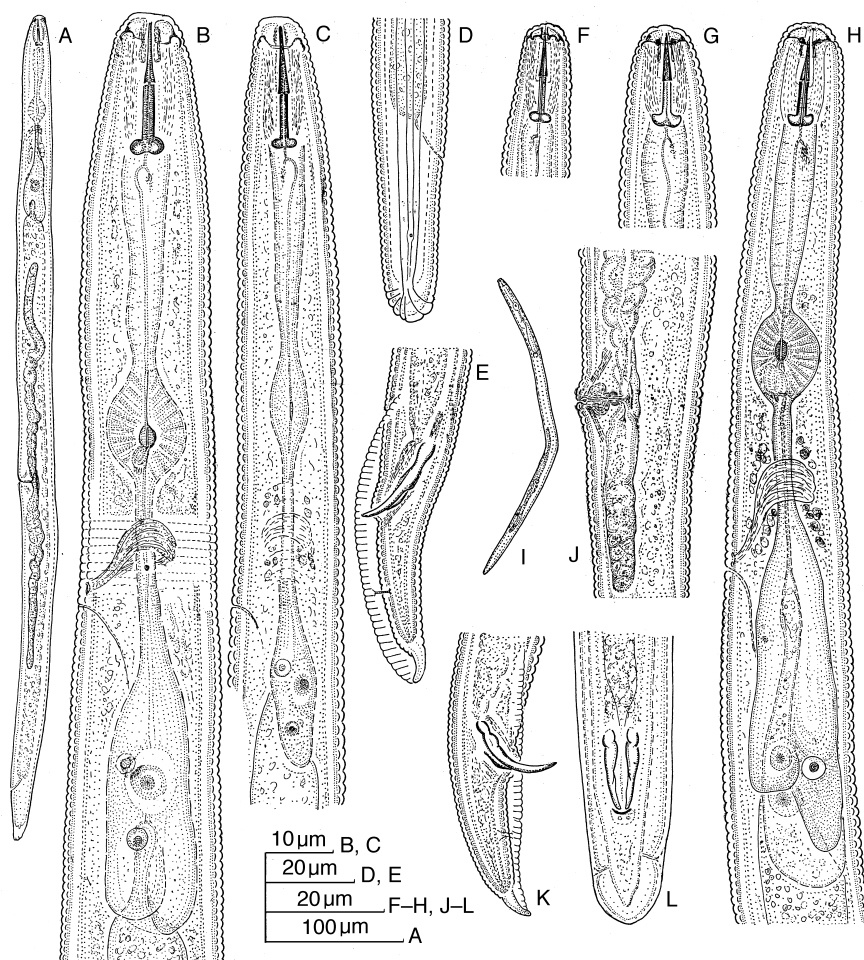
*Scutellonema sexlineatum* Razjivin, 1971

#### Other species

*Pratylenchoides alkani* Y  ksel, 1977

*P. bacilisemenus* Sher, 1970

*P. camachoi* Gomez Barcina, Castillo & Gonzalez Pais, 1990



**Fig. 77.** A–E. *Pratylenchoides crenicauda* Winslow. F–L. *Apratylenchoides belli* Sher. C, E, F, K and L. Males, remainder females. A and B. Lectotype female. C–E. Topotypes. F–L. Paratypes. A and I. Entire females. B, C and H. Oesophageal regions. D, E, K and L. Tail ends. F and G. Head ends. J. Vulval region.

- P. clavicauda* Geraert, Choi & Choi, 1990  
*P. epacris* Eroshenko, 1978  
*P. erzurumensis* Yüksel, 1977  
*P. heathi* Baldwin, Luc & Bell, 1983  
*P. hispaniensis* Troccoli, Vovlas & Castillo, 1997  
*P. katalani* Katalan-Gateva & Aleksiev, 1985  
*P. laticauda* Braun & Loof, 1967  
*P. leiocauda* Sher, 1970

- P. magnicauda* (Thorne, 1935) Baldwin, Luc & Bell, 1983  
 syn. *Anguillulina magnicauda* Thorne, 1935  
*Tylenchorhynchus magnicauda* (Thorne) Filipjev, 1936  
*Amplimerlinius magnicauda* (Thorne) Siddiqi, 1976  
*Pratylenchoides ivanovae* Ryss, 1980
- P. magnicaudoides* Minagawa, 1984
- P. maritimus* Bor & s'Jacob, 1966
- P. megalobatus* Bernard, 1984  
 syn. *Radopholus megalobatus* (Bernard) Ryss, 1988
- P. nevadensis* Talavera & Tobar, 1996
- P. orientalis* Eroshenko & Kazachenko, 1985 (syn. of *P. leiocauda* for Loof, 1991, and Talavera & Tobar, 1996)
- P. riparius* (Andrássy, 1985) Luc, 1986  
 syn. *Hoplorthynchus riparius* Andrássy, 1985
- P. ritteri* Sher, 1970  
 syn. *Radopholus ritteri* (Sher) Vovlas & Inserra, 1978
- P. sheri* Robbins, 1985  
 syn. *Amplimerlinius sheri* (Robbins, 1985) Siddiqi, 1986
- P. utahensis* Baldwin, Luc & Bell, 1983
- P. variabilis* Sher, 1970
- P. vassilevi* Stoyanov & Baicheva, 1988

#### Species incerta sedis

- Pratylenchoides gadeai* Arias Delgado, Jiménez Millán & López Pedregal, 1965 (= sp. inq., see under *Tylenchorhynchus*)

#### Remarks

Luc (1987) regarded *Pratylenchoides* as an euryomorphic genus showing variation in length of the oesophageal glands and retaining several ancestral characters, such as the presence of deirids and a well-developed oesophago-intestinal valve. Talavera & Tobar (1996) synonymized *Pratylenchoides ivanovae* and *P. orientalis* with *P. magnicauda* and *P. leiocauda*, respectively, and suggested that differences between *P. maqsoodi* and *P. crenicauda* were weak.

ETYMOLOGY. From *Pratylenchus*, and Greek *o* + *eidos* = likeness, similar.

The type species was found around grass roots at Harpenden, England. A key to species was given by Baldwin *et al.* (1983) and Talavera & Tobar (1996).

#### Genus *Hoplotylus* s'Jacob, 1960

(Fig. 74, G–K)

#### Diagnosis

Radopholinae. Small-sized (< 1 mm), straight to slightly arcuate when relaxed, marked tapering in posterior region. Sexual dimorphism present in anterior region **with male having higher and asymmetrical head and reduced stylet and oesophagus**. Lateral fields each with four incisures (rarely five), reducing to three in oesophageal



and tail regions. Cephalic region in female rounded or conoid-rounded, continuous. **Stylet in females stout, moderately long (21–29  $\mu\text{m}$ ); basal knobs rounded or with outer margins directed forward** becoming tulip-shaped; in males reduced (12–15  $\mu\text{m}$  long). Orifice of dorsal gland one-tenth to one-fourth stylet length behind stylet base. Median bulb in juveniles and females strongly muscular, oval; in males poorly muscular and spindle-shaped. Oesophageal glands making a fairly long overlap on dorsal and dorsolateral sides of intestine, with dorsal gland nucleus a little behind oesophago-intestinal junction and much anterior to nuclei of subventral glands; glands less developed in male. Vulva in posterior region at 80–90%. Anterior branch of female reproductive organs well developed, outstretched; posterior branch rudimentary or in the form of a uterine sac. Spermatheca round or oval. Female tail conical, two to three anal body widths long, annulated to tip, hyaline portion more than one-fourth of tail length. Male shorter and more slender than female. Testis outstretched. **Bursa moderately developed, subterminal**, with phasmidial extension. Spicules arcuate, pointed. Gubernaculum linear, 25–40% of spicule length, apparently fixed. Endoparasites of roots.

#### Type species

*Hoplotylus femina* s'Jacob, 1960

#### Other species

*Hoplotylus montanus* Minagawa, 1984

*H. silvaticus* Bernard & Niblack, 1982

*H. sjacobi* Bernard & Niblack, 1982

*H. triversus* (Minagawa, 1984) Siddiqi, 1986

syn. *Radopholoides triversus* Minagawa, 1984

*Radopholus triversus* (Minagawa) Luc, 1987

ETYMOLOGY. From the Greek *hoplo* = arming, and *tylos* = knob.

*Hoplotylus femina*, the type species, was found within and around the roots of *Quercus robur* L. and *Chamaecyparis lawsonia* Parl. in The Netherlands. A key to species was given by Minagawa (1988b).

### Genus *Apratylenchoides* Sher, 1973

(Fig. 77, F–L)

#### Diagnosis

Radopholinae. Sexual dimorphism in anterior region very poorly marked. Small-sized (about 0.6 mm or less), slender, straight or slightly arcuate upon relaxation. Lateral field with four incisures, not areolated. **Deirids indistinct**. Phasmids just behind middle of tail. Cephalic region low, flat, continuous, with two to three annules; framework strongly sclerotized in both sexes. Stylet strong but small (15–18  $\mu\text{m}$  in type species), conus about half as long as total stylet length, knobs round, may be anteriorly flattened. **Orifice of dorsal gland one-third to half stylet length behind stylet base**. Median bulb spheroidal, very muscular; oesophageal glands overlapping intestine mostly dorsally and laterally; **one subventral gland**

**forming short ventral overlap**, its nucleus opposite that of dorsal gland and near oesophago-intestinal junction; **three gland nuclei not in tandem**. Oesophago-intestinal junction with a small oval valvula. Vulva posterior (about 77–82%). Ovary single, anteriorly outstretched; **posterior branch rudimentary**. Spermatheca round, axial, with **round sperm** when fertilized. Female tail tapering, about twice anal body width long. Male tail conical, over two anal body widths long, enveloped by a simple, crenate bursa, with phasmidial pseudoribs. Spicules cephalated, small (15–18  $\mu\text{m}$  long in type species). Gubernaculum small.

#### Type species

*Apratylenchoides belli* Sher, 1973

#### Other species

*Apratylenchoides homoglans* Siddiqi, Khan & Reddy, 1991

ETYMOLOGY. Greek privative prefix *a* = without, not, and *Pratylenchoides*.

*Apratylenchoides belli* was found in soil around roots of shadscale (*Atriplex confertifolia* Wats.), 1 mile south of Fairfield, Utah, USA. *Apratylenchoides homoglans* occurred in chrysanthemum roots and soil in Bangalore district, India.

### Genus *Zygradus* Siddiqi, 1991

(Fig. 78)

#### Diagnosis

Radopholinae. Body straight to ventrally arcuate upon fixation, under 1 mm long. **No marked sexual dimorphism in anterior region**. Cuticle annulated. Lateral fields with four incisures. Deirids absent; phasmids pore-like, at or near middle of tail. Cephalic region low, rounded, continuous or slightly offset, with two to three annules; oral disc indistinct, in SEM bow-tie-shaped, with six pit-like labial sensilla at the rim of the oral aperture. Stylet about twice head width long. Median oesophageal bulb oval, muscular. **Oesophageal glands elongated, lying on dorsal side of intestine**. Vulva postmedian. Ovaries paired. Spermathecae axial, rounded. Female tail tapering, three to four anal body widths long; terminus rounded to conoid; **hyaline region at terminus inconspicuous**. Male stylet and oesophagus similar to those of female. Spicules with distal end flanged and opening pore-like, ventrally subterminal. Male tail conical, ventrally arcuate, **completely enveloped by a bursa**.

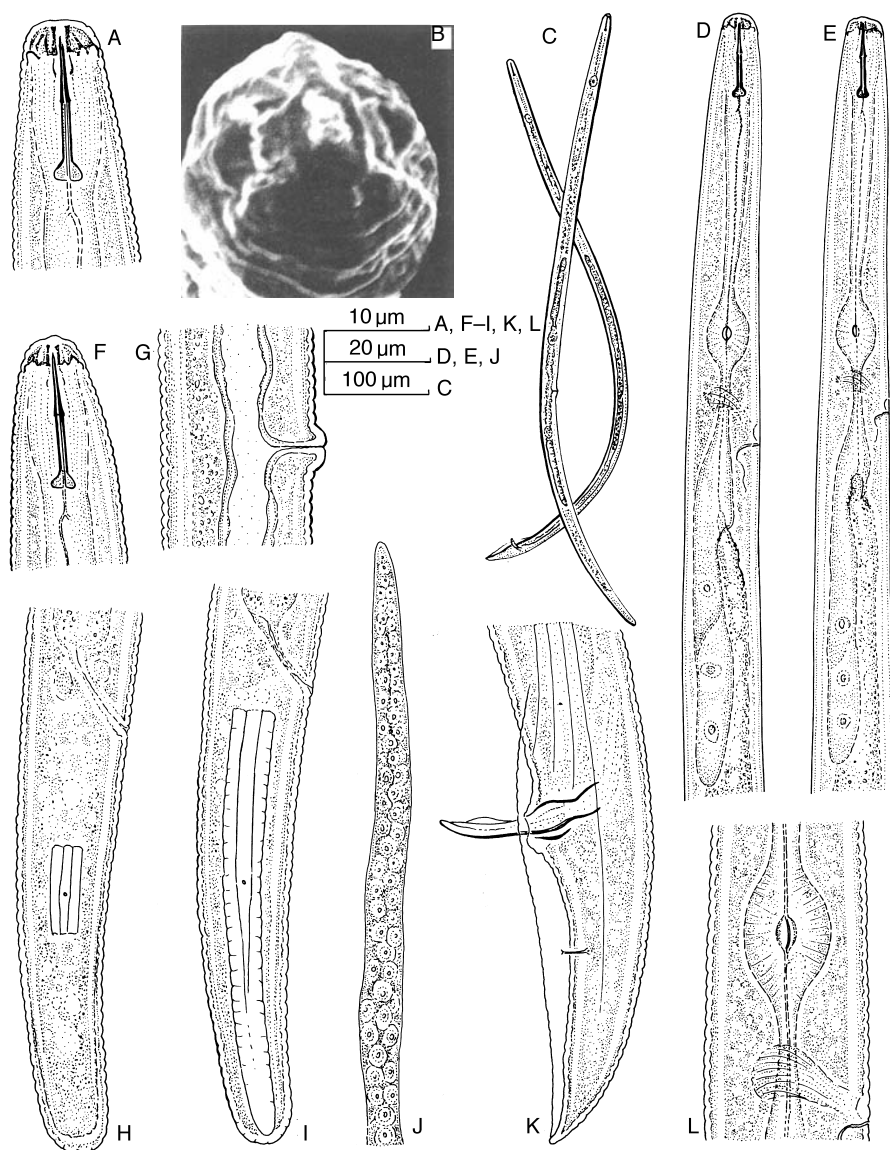
#### Type species

*Zygradus rector* Siddiqi, 1991

#### Other species

*Zygradus nigeriensis* (Sher, 1968) Siddiqi, 1991  
syn. *Radopholus nigeriensis* Sher, 1968

ETYMOLOGY. The generic name is derived from combining the first three letters of *Zygotylenchus* and *Radopholus*, and is masculine in gender.



**Fig. 78.** *Zygradus rector* Siddiqi. A. Head end of female. B. En face view of female. C. Adult male and female. D and E. Oesophagus of female and male, respectively. F. Head end of male. G. Vulva. H and I. Tail ends of female. J. Testis. K. Tail end of male. L. Nerve ring region. (After Siddiqi (1991), courtesy *Afro-Asian Journal of Nematology*.)

The type species was found in forest soil collected about 25 miles east of Ore near Ore-Benin City Road, Nigeria.

## Genus *Achlysiella* Hunt, Bridge & Machon, 1989

(Fig. 79)

### Diagnosis

Radopholinae. Body vermiform except for mature female which becomes elongate-obese. **Marked sexual dimorphism in anterior region.** Cephalic region low, flattened in female, offset, knob-like in male. In SEM, female head shows submedian lips fused with labial disc appearing dumb-bell-shaped and lateral lips extending to base of head (cf. *Radopholus* in which it appears bow-tie-shaped with angular submedian lips). Oesophageal glands in immature female very long, extending dorsally and dorsolaterally over intestine, gland cells discrete. Vermiform female ovary immature, with a few oocytes; tail conoid, with narrow, rounded terminus. **Mature female sausage-shaped** with tapering ends and attenuated neck region; vulva lips protuberant. **Gelatinous egg sac with relatively large eggs, juveniles, adult males and vermiform females present.** Male stylet and oesophagus degenerate; tail conoid, with distinct hyaline region; bursa reaching almost to tail tip. **Juveniles moulting to adult stage without feeding.** Other characters as given for *Radopholus*.

### Type species

*Achlysiella williamsi* (Siddiqi, 1964) Hunt, Bridge & Machon, 1989

syn. *Radopholus williamsi* Siddiqi, 1964

*Radopholus similis* apud Williams, 1960, nec Cobb, 1893

### Other species

*Achlysiella brevicaudata* (Colbran, 1971) Ebsary, 1991

syn. *Radopholus brevicaudatus* Colbran, 1971

*A. capitata* (Colbran, 1971) Ebsary, 1991

syn. *Radopholus capitatus* Colbran, 1971

*A. magniglans* (Sher, 1968) Ebsary, 1991

syn. *Radopholus magniglans* Sher, 1968

*A. trilineata* (Sher, 1968) Ebsary, 1991

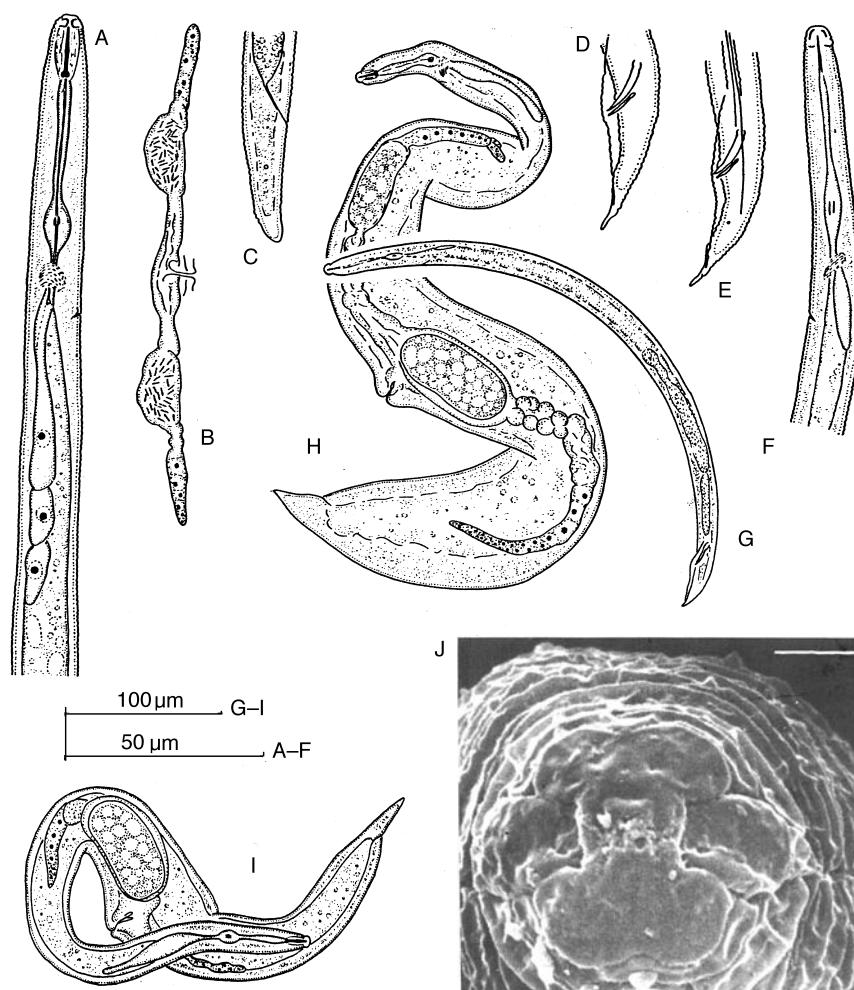
syn. *Radopholus trilineatus* Sher, 1968

*A. vacua* (Colbran, 1971) Ebsary, 1991

syn. *Radopholus vacuus* Colbran, 1971

### Note

*Achlysiella williamsi* is thought to have evolved in the Papua New Guinea region as a parasite of sugarcane and from there it was probably spread to other regions, including Mauritius, by man through the use of infested rooted sugarcane cuttings (Hunt *et al.*, 1989). Hunt *et al.* (1989) while discussing the phylogenetic relationship of *Achlysiella* stated, '*Achlysiella* n. gen. [unlike *Acontylus* of Rotylenchulidae] shares more fundamental morphological characters – the anterior placement of the dorsal oesophageal gland opening, shape of female head, *en face* view, relatively weak development of stylet and labial framework, long conoid tail – with the pratylenchids than with the rotylenchulids and clearly belongs to the Pratylenchidae. *Achlysiella* should be regarded as an intermediate state between the tendency for the endoparasitic females of *Pratylenchus* and *Radopholus* extracted from roots to be



**Fig. 79.** *Achlysiella williamsi* (Siddiqi). A–C. Immature females. D–G. Males. I and H. Mature females. A and F. Oesophageal regions. B. Genital tracts of female. C–E. Tail ends. G–I. Adults. J. Scanning electron micrograph of *en face* of female. (After Hunt *et al.*, 1989.)

more swollen than those from soil (a feature not found in Hoplolaimidae, incidentally) and the more advanced genera where obese females develop a sophisticated trophic nurse-cell system.'

Ryss and Wouts (1997) described *Radopholus nelsonensis* as having mature females slightly swollen, swelling not distorting the general body shape. They noted that the swelling of the female body did not begin until the egg-laying stage commenced and hence regarded the shape of the female body as an unsatisfactory character for generic placement. They were not able to confirm the presence of a

gelatinous egg sac or juveniles moulting to adult stage without feeding, the two characteristics of the genus *Achlysiella*. I have seen some of the gravid females of *R. similis* slightly swollen and moulting juveniles with two superimposed cuticles.

ETYMOLOGY. From *Achlys* = goddess of obscurity in Greek mythology, and *ella* = small. The generic name is feminine in gender.

The type species was found parasitizing sugarcane roots in Mauritius.

## SUBFAMILY NACOBBINAE

### (Monodelphic, endoparasitic and root-gall-inciting Hoplolaimoidea)

This monotypic subfamily Nacobbinae is interesting both taxonomically and biologically. These endoparasitic gall-causing nematodes have been called false root-knot nematodes but they are morphologically different from the *Meloidogyne* spp. Unlike the members of the Hoplolaimidae, the male does not show marked sexual dimorphism in the cephalic region, stylet and oesophagus. However, the stylet of the male is slightly longer and more robust than that of the female – a character found in the Meloidogynidae and Heteroderidae.

Allen (1960) considered *Nacobbus* as a potential member of a group containing *Radopholus*, *Pratylenchoides* and *Pratylenchus*, while the genus *Rotylenchulus* (associated with *Nacobbus* under Nacobbinae by Chitwood, 1950) was thought to have little or no likelihood of being derived from a *Radopholus*- or *Pratylenchoides*-like ancestor, and was regarded as a relative of *Helicotylenchus* of the Hoplolaimidae. Allen (1960) stated that the reduction or loss of the posterior branch of the female gonad and the development of a saccate form by the adult parasitic female of *Nacobbus* were not of more significance than the several characteristics in common with *Radopholus* and its relatives which could be more indicative of phylogenetic relationships.

Golden (1971) recognized the family Nacobbidae for the subfamilies Nacobbinae and Rotylenchulinae and placed it with Heteroderidae in the superfamily Heteroderoidea. Wouts (1979) rejected this on the ground that *Nacobbus* is monodelphic and should not be placed with the heteroderids, which are didelphic. He also argued that the genus, in all characteristics except the female body shape, resembles members of the family Pratylenchidae.

The similarity of *Nacobbus* to *Meloidogyne* in inciting root-galls is remarkable. It appears very likely that *Meloidogyne* and *Meloinema* evolved from a Pratylenchidae-type ancestor, and that these genera have a close relative in *Nacobbus*. However, because of the presence of pseudomonodelphy, a round labial disc separate from lateral lip areas, a normally placed excretory pore, a subterminal vulva lacking a finger-print-like perineal pattern and a bursate male tail, *Nacobbus* should not be placed in the Meloidogynidae. It is here regarded as representing a separate subfamily, Nacobbinae under Pratylenchidae.

Although the root-galls caused by *Nacobbus* spp. look similar to those caused by *Meloidogyne* spp., the structures of the syncytia (giant cells) induced by *Nacobbus* spp. more closely resemble those of the syncytia induced by *Heterodera* spp. However, wall ingrowths typical of the syncytia induced by the species of *Heterodera*

and *Meloidogyne* are absent from the syncytia induced by *Nacobbus* spp. as well as by *Rotylenchulus* spp. (see Jones & Payne, 1977).

*Nacobbus dorsalis* and *N. aberrans* are known from western USA. *Nacobbus serendipiticus bolivianus* (= *N. aberrans*) was described from roots of *Solanum andigena* in Bolivia where it could be a native species. The records of *Nacobbus* on tomato under glass in England and The Netherlands suggest the man-made distribution of this pest. *Nacobbus aberrans* completes its life cycle on sugarbeet in 48 days at 25°C. All juveniles are migratory endoparasites. Only feeding by adults induces syncytia (Inserra *et al.*, 1983).

## Subfamily Nacobbinae Chitwood in Chitwood & Chitwood, 1950

### Diagnosis

Pratylenchidae. **Marked sexual dimorphism in body shape. Mature female saccate, spindle-shaped or batatiform; young female, male and juveniles vermiform. Anterior regions of young female and male similar.** Deirids absent. Phasmids postanal. Cephalic region low, continuous, broadly rounded, annulated; framework strongly sclerotized; labial disc round to oval, protuberant, separate from lip areas; six labial pits on surface around oral opening; six lip areas present (SEM). Stylet well developed, about twice maximum width of cephalic region, with round knobs. Orifice of dorsal gland close to stylet base. Median bulb strongly muscular. **Oesophageal glands elongated, overlapping intestine mostly dorsally; subventral glands asymmetrical, extending beyond the dorsal gland. Vulva near anus. Monodelphic, prodelphic. Postvulval uterine sac absent.** Early mature female with a long tubular uterus and serpentine ovary. Tail of young female short (one to two anal body widths long), rounded. Early juveniles with subcylindrical tail, with small, indistinct, hyaline terminal portion. Male tail conical, arcuate, completely enveloped by a bursa. Spicules well developed, cephalated, arcuate. Gubernaculum small, simple, fixed. Eggs retained in body or laid within gelatinous material. **Mature female obligate sedentary endoparasite inciting root galls; juveniles, young females and males migratory root endoparasites.**

### Type genus

*Nacobbus* Thorne & Allen, 1944

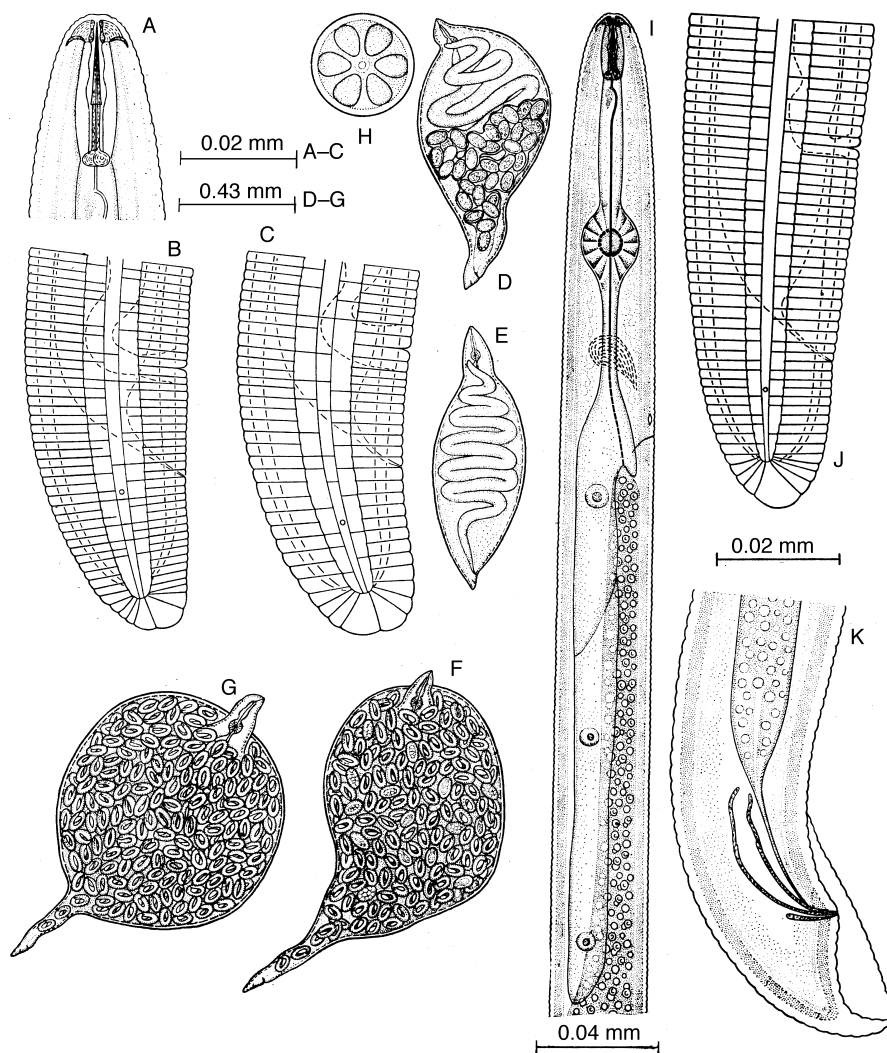
No other genus.

### Genus *Nacobbus* Thorne & Allen, 1944

(Fig. 80)

### Diagnosis

Nacobbinae. **Young female:** Vermiform, elongate-slender, about 1 mm long. Cuticle distinctly annulated. Lateral fields each with four incisures, irregularly areolated. Phasmid pore-like, anterior to middle of tail. Cephalic region broadly rounded, continuous, with three to four annules. Median bulb rounded, with large refractive thickenings. Stylet strong, about 21–25 µm long, conus about as long as posterior part, knobs rounded. Oesophageal glands elongate, extending for more than two body widths; subventral glands asymmetrical, extending past dorsal gland; nuclei of



**Fig. 80.** A–G. *Nacobbus dorsalis* Thorne & Allen. H–K. *Nacobbus aberrans* (Thorne). A. Head end of immature female. B, C and J. Tail ends of immature females. D, F and G. Mature females. E. Early stage of mature female. H. *En face*. I. Oesophageal region. K. Tail end of male. (After Sher (1970a), courtesy *Journal of Nematology*.)

three glands lie in tandem behind oesophago-intestinal junction. Vulva a transverse slit, located within two anal body widths of anus. Ovary immature. Tail tapering to a broadly rounded terminus, one to two anal body widths long. **Migratory in soil and roots.** **Mature female:** Body saccate tapering anteriorly from median bulb and posteriorly from uterine region, often appearing spindle-shaped; early stage of mature female usually batatiform, with subterminal anus and vulva, **very long, tubular uterus,**



and a long, serpentine ovary reaching oesophagus; swollen body may contain several dozen eggs. **Sedentary endoparasites inciting root-galls.** **Male:** Vermiform, with well-developed cephalic sclerotization. Stylet about 23–27  $\mu\text{m}$  long and oesophagus structurally similar to that of immature female. **Oesophageal glands elongated, mostly dorsal to intestine.** Testis single, outstretched. Spicules cephalated, ventrally arcuate, 20–35  $\mu\text{m}$  long. Gubernaculum simple, linear to trough-shaped, fixed. Cloacal lips not modified. Male tail completely enveloped by a bursa.

#### Type species

*Nacobbus dorsalis* Thorne & Allen, 1944

#### Other species

*Nacobbus aberrans* (Thorne, 1935) Thorne & Allen, 1944

syn. *Anguillulina aberrans* Thorne, 1935

*Pratylenchus aberrans* (Thorne) Filipjev, 1936

*N. batatiformis* Thorne & Schuster, 1956

*N. serendipiticus* Franklin, 1959

*N. serendipiticus bolivianus* Lordello, Zamith & Boock, 1961

*N. bolivianus* Lordello, Zamith & Boock, 1961

ETYMOLOGY. Patronym honouring N.A. Cobb.

The type species was found in roots of *Erodium cicutarium* (L.) at Caliente, California, USA. *Nacobbus aberrans* was found on *Atriplex confertifolia* in desert foothills west of Utah Lake, USA, and *N. batatiformis* was described from sugarbeet from Colorado, Nebraska and Wyoming, USA; several species of Cactaceae, Chenopodiaceae, Cruciferae and Zygophyllaceae were found to be susceptible. *Nacobbus serendipiticus* was described from galls of tomato in England. *Nacobbus batatiformis*, *N. serendipiticus* and *N. serendipiticus bolivianus* were synonymized with *N. aberrans* by Sher (1970a) but recognized as valid by Siddiqi (1986).

## FAMILY MELOIDOGYNIDAE

### (Root-knot nematodes)

*Meloidogyne* spp., the root-knot nematodes, are obligate endoparasites of great economic importance. They are one of the major limiting factors in the production of field and plantation crops throughout the tropical and subtropical countries; a few species (e.g. *M. naasi*, *M. artiellia*) are adapted to the temperate region, but develop during the summer months. Vegetables, cereals, banana, sugarcane, tea, coffee, etc., are severely damaged by them and the financial and economic losses can be enormous. As perfect examples of highly adapted root parasitism, these nematodes enjoy a guaranteed continuous supply of food and water from the host and protection within the gall for the females and their progeny.

The infective stage that emerges from the egg is the second-stage juvenile, the first moult occurring within the egg. It has a stored energy supply sufficient for about 1 month's continuous struggle to locate and penetrate a root and establish a feeding

site, usually within the pericycle and vascular tissues. The oesophageal gland secretions injected into the root cells, incite the production of multinucleate giant cells (syncytia, nurse cells, transfer cells), which provide a continuous source of food for the parasite (Fig. 6). A gall is formed at the feeding site due to extensive hypertrophy and hyperplasia of the root cells. The juvenile feeds, grows and becomes sausage-shaped in 2–3 weeks. It undergoes three further moults, the third and fourth moults occurring within the cuticle of the second moult. The third- and fourth-stage juveniles do not have a stylet and cannot feed. A stylet reappears after the fourth moult, and the adult female commences feeding. It becomes spheroidal and after about 15–30 days of feeding and growth starts laying a large number of eggs in a gelatinous material secreted by the rectal gland cells through the anus, located next to the vulva at the posterior end. The gelatinous matrix of *Meloidogyne* shows pectolytic, cellulytic and proteolytic enzymatic activity on plant cells; the cell lysis activity of the matrix forms a canal from the female posterior end to the root-gall surface (Orion & Franck, 1991).

Eggs are deposited in the gelatinous matrix and large egg masses are produced within and outside the induced galls that turn brownish and become shrivelled when dried, but the eggs in them remain viable for a long time. The eggs hatch on exposure to moisture and stimulus from exudates from host roots. The vermiform male develops from a sausage-shaped juvenile. Males probably do not feed, but survive only to fertilize the females. During adverse conditions most of the developing juveniles become males.

The damage to plants is due largely to the disruption of vascular tissues and extensive hypertrophy and hyperplasia of root cells. Besides the knotted roots, an infected plant shows poor growth, unthriftiness and generally wilt symptoms. The damage is aggravated by the parasite's interaction with other microorganisms such as fungi (species of *Fusarium*, *Rhizoctonia*, *Phytophthora*, *Pythium*, *Curvularia*, etc.) and bacteria (*Pseudomonas*, *Agrobacterium*, etc.). *Pasteuria penetrans*, *Paecilomyces lilacinus*, *Arthrobotrys conoides*, *Arthrobotrys oligospora*, *Arthrobotrys musiformis* and *Verticillium chlamydosporium* found in the soil are natural enemies of root-knot nematodes and can be used as biopesticides (Cabanilla & Barker, 1989; Stirling, 1991; Mousa *et al.*, 1995, etc.).

*Meloidogyne mayaguensis* parasitizes coffee in Cuba and occurs sympatrically with and is more damaging than *Meloidogyne incognita*, *M. arenaria* and *M. javanica* (Rodriguez *et al.*, 1995). It completes its life cycle in 32–42 days at 25–30°C. Severe root galling due to *M. mayaguensis* was observed on commercial guava (*Psidium guajava*) in Nelspruit, South Africa. The attacked trees declined severely or died within 3 years (Willers, 1997).

*Meloidogyne acronea* is a parasite of cotton (*Gossypium hirsutum* L.) and is indigenous to semi-arid parts of southern Africa. Its occurrence with the natural habitat of *Gossypium herbaceum* var. *africanum* in this region suggests that there might have been co-evolution between the two species (Page & Bridge, 1994). *Meloidogyne citri* and *M. mingnanica* parasitize citrus in China, while *M. indica* parasitizes citrus in India. *Meloidogyne exigua* is a parasite of coffee in Central and South America, where it is widely distributed. *M. coffeicola* attacks coffee in Brazil.

All the species listed in the first edition of this book under the subgenus *Hypsoperine* parasitize monocots, mostly grasses. *Meloidogyne graminis* is a parasite of

St Augustine grass, *Stenotaphrum secundatum* (Walt.) in Florida, USA. The galls are in the form of slight swellings and the posterior of the females often protrudes by rupturing root tissues. It does not develop when inoculated to tomato, squash, maize, carrot, grapefruit and peach, but multiplies readily on grasses. *Meloidogyne ottersoni* parasitizes canary grass and *Phalaris arundinacea* (L.) in Wisconsin, USA while *M. acronea* is a parasite of *Sorghum vulgare*, *Pennisetum glaucum* and grasses such as *Eragrostis* spp. and *Chloris gayana* in South Africa. *Meloidogyne propora* was found parasitizing roots of *Cyperus obtusiflorus*, Ile Picard, Aldabra Atoll in the West Indian Ocean where it also parasitizes *Casuarina equisetifolia* L. No galling of roots was observed on *Cyperus* or *Casuarina* but slight galling occurred when cultured on *Solanum nigrum*. The heads of the females were directed away from the root tip and most of the swollen body was exposed (Spaull, 1977).

Chitwood (1949) did much towards the identification and taxonomy of *Meloidogyne* spp. He re-established the genus *Meloidogyne* of Goeldi (1887), published in 1892, and showed that the perineal pattern of females was an important diagnostic characteristic for the differentiation of the species. Today the species identification is based largely on the perineal patterns and juvenile characteristics. Esser *et al.* (1976) gave a compendium for the identification of 32 species and Franklin (1979) gave distinguishing characters of *Meloidogyne* and listed 36 valid species. Hirschmann (1984) listed 49 species and a subspecies of *Meloidogyne* as valid. CAB International produced a CD-ROM database edited by Eisenback in 1997.

Several *Meloidogyne* species are able to reproduce by mitotic parthenogenesis. Some species are polyploids, e.g. *M. javanica* ( $2n = 43-48$ ) as compared to *M. hapla* ( $n = 6$  or  $10-17$ ). *Meloidogyne carolinensis*, *M. graminicola* and *M. naasi* have  $n = 18$ , the basic chromosome number for *Meloidogyne*. The higher or lower chromosome number resulting due to polyploidy or aneuploidy produces species complexes.

From the studies made on the chromosome numbers in *Meloidogyne*, *Spartonema* and related genera, some patterns of karyotic evolution are apparent (Triantaphyllou, 1983), although the data available so far are meagre. The probable basic numbers are: *Meloidogyne*  $n = 18$ , *Spartonema spartinae*  $n = 7$ , *Heterodera*  $n = 9$ , *Meloidodera*  $3n = 27$ . Most *Meloidogyne* and *Meloidodera* are parthenogenetic while most *Heterodera* and *Hypsoperine* are amphimictic; cross-fertilization, particularly when males are abundant, is suspected for parthenogenetic species. In fact only a few species of *Meloidogyne* are exclusively amphimictic (e.g. *M. carolinensis*); most reproduce by parthenogenesis or by a combination of parthenogenesis and amphimixis.

Polyploidy may result in different chromosomal forms within one species. For example, *Meloidogyne incognita* and *M. arenaria* each have two forms, one diploid ( $2n = 32-36$  for the former,  $34-37$  for the latter) and another triploid ( $3n = 40-46$  for the former,  $50-56$  for the latter). A recently described species, *M. paranaensis*, has  $3n=50-52$  and reproduces by mitotic parthenogenesis (Carneiro *et al.*, 1996). The great morphological and physiological variabilities of the parthenogenetic *Meloidogyne* species have produced species complexes involving the so-called sibling species. Protein electrophoresis (enzyme polymorphism, isoenzyme analysis) is helping to distinguish between such species and in tracing their phylogeny (Dickson *et al.*, 1971; Dalmasso & Bergé, 1983, etc.).

The polymerase chain reaction–restriction fragment length polymorphism (PCR–RFLP) analysis based on individual second-stage juveniles was useful in the identification of ten Japanese *Meloidogyne* species (Orui, 1998). On the analysis of total soluble proteins using two-dimensional gel electrophoresis (2-DGE) and total genome DNA using electrophoresis of amplified fragment length polymorphisms (AFLP), *M. hapla* race A and race B clustered together, the three tropical species *M. incognita*, *M. javanica* and *M. arenaria* formed another cluster, and the species specialized on Gramineae, *M. naasi*, *M. chitwoodi* and *M. fallax*, were distant from the rest, with high similarity between *M. chitwoodi* and *M. fallax*. But dendrograms based on morphological data were different from those based on molecular data, particularly for *M. incognita* and *M. naasi* (Beek *et al.*, 1998).

Meloidogynidae and Heteroderidae most probably originated from ancestors similar to the contemporary, migratory Pratylenchidae and Hoplolaimidae, respectively. Coomans (1979) believed that Meloidogynidae and Heteroderidae had a common tylenchid ancestor, the former representing the apomorphic branch with several derived characters such as the anterior shifting of the excretory pore, absence of a stylet and of feeding in third- and fourth-stage juveniles, a basic chromosome number  $n = 18$  and the formation of the root-galls. Two subfamilies were recognized by him: Meloidogyninae and Nacobboderinae, with a further division of Meloidogyninae into two tribes, Meloidogynini and Meloidoderellini. Nacobboderinae shows several plesiomorphic characters and is more ancestral than Meloidogyninae (Coomans, 1979; Husain, 1976). It is related to Nacobbinae and Rotylenchulinae, linking the Pratylenchidae and Hoplolaimidae with the Heteroderidae (Golden & Jensen, 1974; Siddiqi, 1980).

## Family Meloidogynidae Skarbilovich, 1959 (Wouts, 1973)

### Diagnosis

Hoplolaimoidea. **Root-gall-inciting, female feeding incites multinucleate nurse cells.** Marked sexual dimorphism present. Cuticle striated. Lateral fields each with four or five incisures. **Cephalic region low, with one to four annules.** In SEM, **female labial disc dorso-ventrally elongated, dumb-bell-shaped** with oral opening a small round pore surrounded by six inner labial pits (sensilla). Framework moderately sclerotized, hexaradiate; **lateral sectors equal to or wider than submedians.** Stylet moderately strong, **male stylet longer and more robust than that of female.** Orifice of dorsal oesophageal gland closely behind stylet base. Median oesophageal bulb oval or round, with large refractive thickenings. Oesophageal glands elongated, extending over intestine mostly ventrally, but also laterally; subventrals asymmetrical, extending past the dorsal gland, SVN always behind DN. **Excretory pore in female opposite or anterior to median bulb**, in male usually behind median bulb. **No preadult vermiform female stage** except in *Meloinema*. **Mature female:** Swollen, sedentary, round, oval to pear-shaped with a projecting neck. Cuticle moderately thick, striated, generally forming typical, **finger-print-like perineal pattern** terminally. **No cyst stage.** **Vulva subterminal or terminal.** Anus near vulval lip; tail rudimentary or absent. Stylet under 25  $\mu\text{m}$  long but in *Meloinema* 30–35  $\mu\text{m}$  long. Median bulb oval or rounded, usually offset, with large refractive thickenings. **Didelphic-prodelphic; ovaries coiled.** Most eggs laid. **Large rectal glands which**

**secrete gelatinous matrix present**; latter extruded through anus. **Male:** Vermiform, migratory, generally non-plant-feeding, over 1 mm long, posterior end twisted through 90–180°, develops by metamorphosis within a saccate juvenile. Cephalic region rather low and continuous; amphids large transverse slits; labial cap large, prominent; framework moderately sclerotized, **lateral sectors wider than submedians**. Stylet strong, usually over 20 µm long, knobs prominent. **Tail short, lacking a bursa or absent** (except *Bursadera*). Spicules large (25–64 µm), pointed distally. Gubernaculum linear to trough-shaped, not protrusible. Cloacal lips non-tuboid, generally with hypopygium. **Juveniles:** Second stage hatches, is migratory and infective. Third- and fourth-stage juveniles swollen, without stylet in type genus. In *Meloinema* third- and fourth-stage juveniles vermiform. Cephalic region low, anteriorly flattened or rounded. **Lateral sectors wider than submedians**, labial disc distinct in type genus. Stylet weak to moderately developed, less than 20 µm long in type genus, strongly developed in *Meloinema*. Tail elongate-conical, with minutely rounded tip and conspicuous terminal hyaline portion. Phasmids dot-like on tail, usually anterior to middle.

#### Type subfamily

Meloidogyninae Skarbilovich, 1959

#### Other subfamily

Nacobboderinae Golden & Jensen, 1974

#### Remarks

Meloidogynidae differs from Heteroderidae by its members inciting root-galls and having lateral sectors of labial framework being wider than the submedians, weaker cephalic sclerotization and stylet, excretory pore of mature female located opposite or anterior to median bulb and third- and fourth-stage juveniles lacking a stylet in the type genus.

#### Key to subfamilies of Meloidogynidae

1. Preadult female and female juveniles of third and fourth stage saccate;  
mature female with anus at base of dorsal lip of vulva; male tail  
hemispherical ..... **Meloidogyninae**
- Preadult female and female juveniles of third and fourth stage vermiform;  
mature female with anus at some distance from base of dorsal lip of vulva;  
male tail conoid-rounded ..... **Nacobboderinae**

#### Subfamily Meloidogyninae Skarbilovich, 1959

**syn. Meloidogynini Skarbilovich (Coomans, 1979)**

**Meloidoderellinae Husain, 1976**

**Meloidoderellini Husain (Coomans, 1979)**

#### Diagnosis

Meloidogynidae. Root-gall-inciting nematodes. Cephalic region often non-annulated, with a distinct labial disc which is fused with medial and lateral lip sectors. Framework lightly sclerotized, six-sectored with lateral sectors equal to or wider

than submedians. **Stylet** in juveniles and females weak. **Third- and fourth-stage juveniles** saccate, develop within second-stage cuticle, lacking stylet. No preadult vermiform stage. Females saccate, round to pear-shaped, with a short neck; not cyst-forming. **Perineal cuticular pattern** of striae present. Vulva terminal. **Anus** dorsal at base of dorsal vulval lip; tail absent, or indicated by a slight protuberance of body. Didelphic, prodelphic; ovaries coiled. Excretory pore anterior to median oesophageal bulb, usually near stylet base. **Rectal glands** (not well developed in *Spartonema*) produce gelatinous matrix, expelled through the anus; eggs laid in gelatinous matrix appearing as egg masses. Male cephalic region low, with a large lip cap. **Development** by metamorphosis. Testis single or paired. **Male tail end** twisted; tail less than one anal body width long, rounded; bursa absent.

#### Type genus

*Meloidogyne* Goeldi, 1892

#### Other genus

*Spartonema* Siddiqi, 1986

#### Key to genera of Meloidogyninae

1. Rectal glands in female enormously developed; eggs laid in a gelatinous matrix forming egg sac; second-stage juveniles under 0.6 mm long ..... *Meloidogyne*  
Rectal glands in female not developed; eggs laid singly in plant tissue, egg sac not formed; second-stage juveniles 0.6–0.9 mm long ..... *Spartonema*

#### Genus *Meloidogyne* Goeldi, 1892

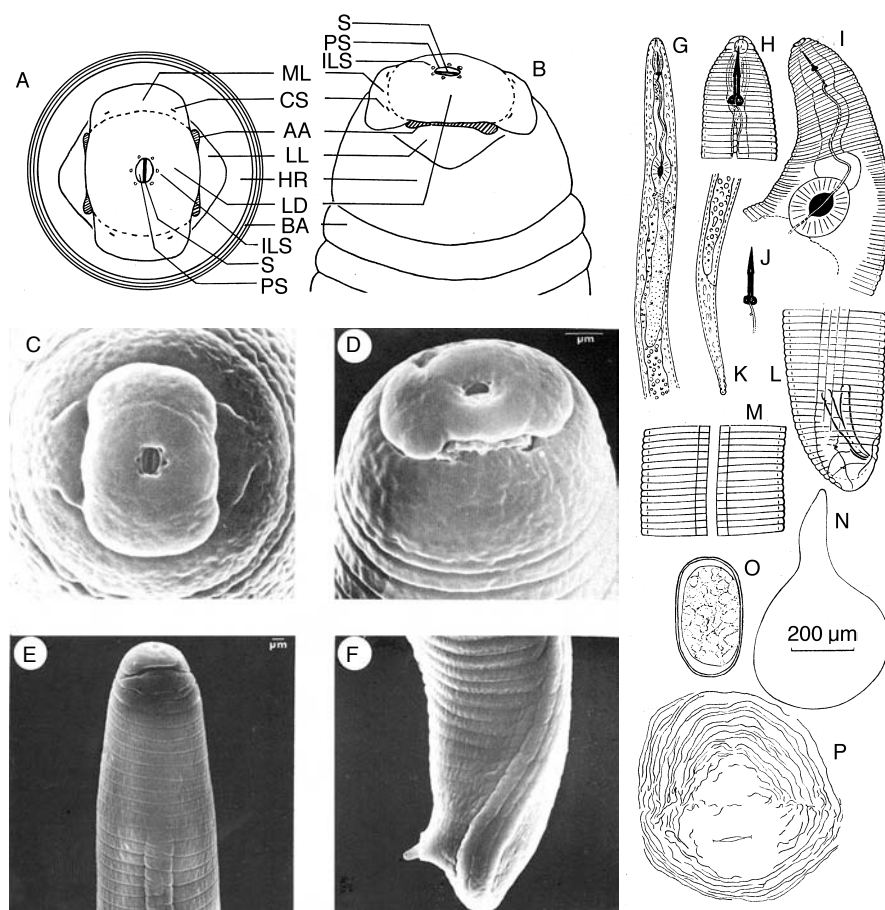
syn. *Hypsoperine* Sledge & Golden, 1964

*Hypsoperine* (*Hypsoperine*) (Siddiqi, 1986)

(Figs 8(b)A; 15, A; 81; 82, A–H)

#### Diagnosis

Meloidogyninae. Root-gall-inciting. **Mature female:** Round to pear-shaped with short projecting neck, white, sedentary. **No cyst stage.** Vulva and anus close together, terminal; **perineum** with a fingerprint-like cuticular pattern, elevated in some species previously assigned to *Hypsoperine*. Phasmidial apertures dot-like, slightly above and on either side of anus. **Cuticle** thick, striated. Stylet slender, generally 12–15 µm long, with small knobs. **Excretory pore** anterior to median bulb, often close behind base of stylet. Ovaries paired prodelphic, convoluted. Rectal glands six, large, secrete gelatinous material in which eggs are deposited; eggs not retained in body. **Male:** Vermiform, up to 2 mm long, tail end twisted, develops by metamorphosis within a swollen juvenile. Cuticle strongly annulated; **lateral field** with four incisures. **Cephalic region** rounded, not sharply offset, with distinct labial disc and few (one to three) annules; **lateral sectors** wider than submedians, appear as ‘cheeks’. Stylet robust (18–25 µm), with large knobs. Oesophageal glands mostly ventral to intestine. Spicules slender, generally 25–33 µm long, gubernaculum 7–11 µm long. **Testis** single, or paired when sex reversal occurs. Tail rounded. Phasmids dot-like, near cloacal aperture, which is subterminal. Bursa absent. **Juveniles:** First stage with a blunt tail tip, moults within the egg; second and third



**Fig. 81.** A and B. Head of *Meloidogyne* male, *en face* and lateral view, respectively (diagrammatic). C and D. Scanning electron micrographs of head of *Meloidogyne hapla* Chitwood, race A. E and F. Scanning electron micrographs of head and tail ends, respectively, of *Meloidogyne* male. G–P. *Meloidogyne exigua* Goeldi. G and K. Anterior and posterior regions of second-stage juvenile. H and I. Head ends of male and female, respectively. J. Stylet of male. L and M. Lateral field in tail and midbody regions of male respectively. N. Female. O. Egg. P. Perineal pattern of female. AA, amphidial aperture; BA, body annule; CS, cephalic sensillum; HR, head region; ILS, inner labial sensillum; LD, labial disc; LL, lateral lip; ML, medial lip; PS, prestoma; S, stoma. (A–F. After Eisenback & Hirschmann (1980), courtesy *Journal of Nematology*. G–P. After Lordello & Zamith (1958), courtesy Helminthological Society of Washington.)

moults occurring within the cuticle of second stage. **Second stage:** Vermiform, migratory, infective. Body straight to arcuate upon death, usually under 0.6 mm long. Cephalic region generally rounded with one to four coarse annules, a **distinct labial disc**, framework **lightly sclerotized**, lateral sectors wider than submedians,

**stylet slender, under 20  $\mu\text{m}$** , excretory pore posterior to hemizonid. Tail with conspicuous hyaline region, tip narrow and irregular in outline. **Third stage:** sedentary, **swollen**, sausage-shaped with a short blunt tail. **Stylet absent.** **Fourth stage:** sedentary, swollen, with terminal anus. **Stylet absent.** **Basic haploid chromosome number 13–19.**

#### Type species

*Meloidogyne exigua* Goeldi, 1892

syn. *Heterodera exigua* (Goeldi) Marcinowski, 1909

#### Other species

*Meloidogyne acronea* Coetzee, 1956

syn. *Hypsoperine acronea* (Coetzee) Sledge & Golden, 1964

*Hypsoperine* (*Hypsoperine*) *acronea* (Coetzee) Sledge & Golden, 1964  
(Siddiqi, 1986)

*M. actinidae* Li & Yu, 1991

*M. africana* Whitehead, 1960

*M. aquatilis* Ebsary & Eveleigh, 1983

*M. arabidicida* López & Salazar, 1989

*M. ardenensis* Santos, 1968

syn. *Meloidogyne deconincki* Elmiligy, 1968 (syn. by Karssen & Hoenselaar, 1998)

*Meloidogyne litoralis* Elmiligy, 1968 (syn. by Karssen & Hoenselaar, 1998)

*M. arenaria* (Neal, 1889) Chitwood, 1949

syn. *Anguillula arenaria* Neal, 1889

*Tylenchus arenarius* (Neal) Cobb, 1890

*Heterodera arenaria* (Neal) Marcinowski, 1909

*Meloidogyne arenaria arenaria* (Neal) Chitwood, 1949

*M. artiellia* Franklin, 1961

*M. brevicauda* Loos, 1953

*M. californiensis* Abdel-Rahman & Maggenti, 1987 (nom. nud. in Abdel-Rahman (1981))

*M. camelliae* Golden, 1979

*M. caraganae* Shagalina, Ivanova & Krall, 1985

*M. carolinensis* Eisenback, 1982 (*M. carolinensis* Fox, 1967 = nomen nudum)

*M. chitwoodi* Golden, O'Bannon, Santo & Finley, 1980

*M. christiei* Golden & Kaplan, 1986

*M. cirricauda* Zhang & Weng, 1991

*M. citri* Zhang, Gao & Weng, 1990 (*Nematological Abstracts* **63**, No. 383 gives authors as Shaosheng, Rixia & Ziming, 1990)

*M. coffeicola* Lordello & Zamith, 1960

syn. *Meloidodera coffeicola* (Lordello & Zamith) Kirjanova, 1963

*M. cruciani* Garcia-Martinez, Taylor & Smart, 1982

*M. cynariensis* Fam-Tkhan-Bin, 1990

*M. decalineata* Whitehead, 1968

*M. duytsi* Karssen, Aelst & Van der Putten, 1998

*M. enterolobii* Yang & Eisenback, 1983

*M. ethiopica* Whitehead, 1968



- M. fallax* Karssen, 1996  
*M. fangzhiensis* Chen, Peng & Zheng, 1990  
*M. fujianensis* Pan, 1985  
     syn. *Meloidogyne fujianensis* Cangsang, Jing & Shengyuan, 1988  
*M. graminicola* Golden & Birchfield, 1965  
*M. graminis* (Sledge & Golden, 1964) Whitehead, 1968  
     syn. *Hypsoperine graminis* Sledge & Golden, 1964  
     *Hypsoperine* (*Hypsoperine*) *graminis* Sledge & Golden, 1964 (Siddiqi, 1986)  
*M. hainanensis* Liao JinLing & Feng ZhiXin, 1995  
*M. hapla* Chitwood, 1949  
*M. hispanica* Hirschmann, 1986  
*M. ichinohei* Araki, 1992  
*M. incognita* (Kofoed & White, 1919) Chitwood, 1949  
     syn. *Oxyuris incognita* Kofoed & White, 1919  
     *Heterodera incognita* (Kofoed & White) Sandground, 1923  
     *Meloidogyne incognita incognita* (Kofoed & White) Chitwood, 1949  
     *Meloidogyne acrita* Chitwood, 1949  
     *Meloidogyne incognita acrita* Chitwood, 1949  
     *Meloidogyne elegans* da Ponte, 1977 (syn. of *M. incognita incognita* for Jepson, 1987)  
     *Meloidogyne grahami* Golden & Slana, 1978  
     *Meloidogyne incognita grahami* Golden & Salana, 1978 (Jepson, 1987)  
     *Meloidogyne incognita inornata* Lordello, 1956  
     *Meloidogyne inornata* Lordello, 1956  
     *Meloidogyne kirjanovae* Terenteva, 1965 (syn. by Karssen & Hoenselaar, 1998)  
     *Meloidogyne wartellei* Golden & Birchfield, 1978  
     *Meloidogyne incognita wartellei* Golden & Birchfield, 1978  
*M. indica* Whitehead, 1968  
*M. javanica* (Treub, 1885) Chitwood, 1949  
     syn. *Heterodera javanica* Treub, 1885  
     *Tylenchus* (*Heterodera*) *javanicus* (Treub) Cobb, 1890  
     *Anguillula javanica* (Treub) Lavergne, 1901  
     *Meloidogyne javanica javanica* (Treub) Chitwood, 1949  
     *Meloidogyne javanica bauruensis* Lordello, 1956  
     *Meloidogyne bauruensis* Lordello, 1956 (Esser, Perry & Taylor, 1976)  
     *Meloidogyne lordelloi* da Ponte, 1969  
     *Meloidogyne lucknowica* Singh, 1969  
*M. jianyangensis* Yang, Hu, Chen & Zhu, 1990  
*M. jinanensis* Zhang & Su, 1986  
*M. konaensis* Eisenback, Bernard & Schmitt, 1995  
*M. kongi* Yang, Wang & Feng, 1988  
*M. kralli* Jepson, 1984  
*M. lini* Yang, Hu & Zhu, 1988  
*M. lusitanica* Abrantes & Santos, 1991  
*M. mali* Itoh, Ohshima & Ichinohe, 1969  
*M. maritima* Jepson, 1987  
*M. marylandi* Jepson & Golden in Jepson, 1987

- M. mayaguensis* Rammah & Hirschmann, 1988  
*M. megadora* Whitehead, 1968  
*M. megatyla* Baldwin & Sasser, 1979  
*M. mersa* Siddiqi & Booth, 1991  
     syn. *Meloidogyne (Hypsoperine) mersa* Siddiqi & Booth, 1991  
*M. microcephalus* Cliff & Hirschmann, 1984 (original spelling *microcephala*)  
*M. microtyla* Mulvey, Townshend & Potter, 1975  
*M. mingnanica* Zhang, 1993  
*M. moroccensis* Rammah & Hirschmann, 1990  
*M. naasi* Franklin, 1965  
*M. nataliae* Golden, Rose & Bird, 1981  
*M. oryzae* Maas, Sanders & Dede, 1978  
*M. oteifai* Elmiligy, 1968 (original spelling *oteifae*)  
*M. ottersoni* (Thorne, 1969) Franklin, 1971  
     syn. *Hypsoperine ottersoni* Thorne, 1969  
         *Hypsoperine (Hypsoperine) ottersoni* Thorne, 1969 (Siddiqi, 1986)  
*M. ovalis* Riffle, 1963  
*M. paranaensis* Carneiro, Carneiro, Abrantes, Santos & Almeida, 1996  
*M. partityla* Kleynhans, 1986  
*M. petuniae* Charchar, Eisenback & Hirschmann, 1999  
*M. pini* Eisenback, Yang & Hartman, 1985  
*M. platani* Hirschmann, 1982  
*M. propora* Spaull, 1977  
     syn. *Hypsoperine propora* (Spaull, 1977) Siddiqi, 1986  
         *Hypsoperine (Hypsoperine) propora* (Spaull) Siddiqi, 1986  
*M. querciana* Golden, 1979  
*M. salasi* Lopez-Chaves, 1985  
*M. sasseri* Handoo, Huettel & Golden, 1994  
*M. sewelli* Mulvey & Anderson, 1980  
*M. sinensis* Zhang, 1983  
*M. subarctica* Bernard, 1981  
*M. suginamiensis* Toida & Yaegashi, 1984  
*M. tadshikistanica* Kirjanova & Ivanova, 1965  
*M. thamesi* Chitwood in Chitwood, Specht & Havis, 1952 (Goodey, 1963)  
     syn. *Meloidogyne arenaria thamesi* Chitwood in Chitwood, Specht & Havis, 1952  
*M. trifoliophila* Bernard & Eisenback, 1997  
*M. triticoryzae* Gaur, Saha & Khan, 1993  
*M. turkestanica* Shagalina, Ivanova & Krall, 1985  
*M. vandervegti* Kleynhans, 1988

### Species inquirendae

- Meloidogyne marioni* (Cornu, 1879) Chitwood & Oteifa, 1952  
     syn. *Anguillula marioni* Cornu, 1879  
         *Heterodera marioni* (Cornu) Marcinowski, 1909  
         *Meloidogyne goeldi* Lordello, 1951 (= nom. nov. for *M. marioni*)  
*M. megriensis* (Poghossian, 1971) Esser, Perry & Taylor, 1976 (sp. inq. for Karssen & Hoenselaar, 1998)

- syn. *Hypsoperine megriensis* Poghossian, 1971  
*Hypsoperine* (*Hypsoperine*) *megriensis* Poghossian, 1971 (Siddiqi, 1986)  
*M. poghossianae* Kirjanova, 1963  
 syn. *Meloidogyne acronea* apud Poghossian, 1961  
*M. vialae* (Lavergne, 1901) Chitwood & Oteifa, 1952  
 syn. *Anguillula vialae* Lavergne, 1901  
*Heterodera vialae* (Lavergne) Marcinowski, 1909

## Remarks

The genus *Caconema* was proposed by Cobb (1924) for *Heterodera radiculicola* (Greeff) Müller as type species. Cobb (1924) characterized the new genus thus: 'Resembling *Heterodera*, but truly endoparasitic and less specialized in its parasitism; having the amphids protected by "cheeks"; the males with two testes, instead of one, as in *H. schachtii*, the type species of *Heterodera*.' This statement and his illustrations of the head and amphids clearly indicate that he was dealing with a *Meloidogyne* species. *Caconema* was, therefore, treated as a synonym of *Meloidogyne* by later workers. However, the type species of *Caconema* is *C. radiculicola* (Greeff) which is also the type species of *Subanguina* Paramonov, 1967. *Caconema* and *Subanguina* thus become objective synonyms and the synonymy of *Caconema* with *Meloidogyne* should be rejected (see also notes under *Subanguina*).

Whitehead (1968), Franklin (1971), Esser *et al.* (1976) and some other authors considered *Hypsoperine* a junior synonym of *Meloidogyne*. Golden (1971) regarded *Hypsoperine* as an intermediate genus between *Meloidogyne* and *Cryphodera*, and Thorne & Malek (1968) upheld the validity of the genus by emphasizing the biological aspects of *Hypsoperine*. Siddiqi (1986) agreed with Golden's (1971) statement – 'Its inclusion here and in the key might encourage further study rather than considering these forms as common species of *Meloidogyne*.' *Hypsoperine* and *Spartonema* were synonymized with *Meloidogyne* by Jepson (1987). *Hypsoperine* as a genus or subgenus has not been recognized by recent workers, although Gaur *et al.* (1996) showed some cytogenetic differences between the species of *Meloidogyne* and *Hypsoperine* using polymerase chain reaction–restriction fragment length polymorphism (PCR–RFLP) of ribosomal DNA and suggested that the differences in RFLP pattern corresponding to the two groups provided a basis for a re-examination of their taxonomic status. Nevertheless, the morphological and biometric differences are such that the two genera are not sufficiently different from each other. *Hypsoperine* is here considered as a junior synonym of *Meloidogyne*.

On the other hand, *Hypsoperine* (*Spartonema*) *spartinae* shows several morphological differences, e.g. large juveniles with three incisures in the lateral field, males with a conoid cephalic region and females with a thin cuticle and eggs laid free in root tissues. These characters plus the haploid chromosome number being 7 show that *H. (Spartonema) spartinae* is close to the ancestral form of *Meloidogyne*. *Spartonema* is considered here as a valid genus.

*Spartonema spartinae* is a parasite of smooth cordgrass, *Spartina alterniflora* Loiselius, in South Carolina and Florida, USA. The feeding position in roots is parallel to the root axis with the head directed away from the root apex. Very little or no gelatinous matrix is produced by the females which lay their eggs singly in the plant tissues. *Spartonema spartinae* and *S. kikuyensis* have  $n = 7$  chromosomes and

these species are about twice the size of *Meloidogyne* spp. The two species seem to have followed the same or a similar pathway of cytological evolution, unlike the *Meloidogyne* spp., which have haploid chromosome numbers of 13–19. The haploid number of 16, 17 or 18 of *Meloidogyne* spp. shows that they are tetraploids and that the ancestral species had 8 or 9, rather than 7 chromosomes (Triantaphyllou, 1990).

ETYMOLOGY. Greek *mélon* = apple, fruit, *eidós* = shape, resembling, and *gyné* = female.

The type species was originally found on a coffee plant in Brazil by Goeldi (1887) (published in 1892). Keys to *Meloidogyne* spp. were given by Jepson (1987) and Karssen & Hoenselaar (1998), and on a CD-ROM database by Eisenback (1997).

### Genus *Spartonema* Siddiqi, 1986

syn. *Hypsoperine* (*Spartonema* Siddiqi, 1986)

(Fig. 82, I–P)

#### Diagnosis

Meloidogyninae. **Mature female:** Body oval or lemon-shaped, with a short neck and terminal protuberance on which vulva and anus are located, 0.6–1.1 mm long, width 0.27–0.87 mm in type species. **Cuticle thin.** Cephalic region offset. Stylet 11–17  $\mu\text{m}$  long in type species. Perineal pattern present. **Rectal glands not developed; very little or no gelatinous matrix is produced.** Eggs laid singly in root tissues, egg sac not formed. **Male:** Body 1.7–2.6 mm long; stylet 16–21  $\mu\text{m}$  and spicules 25–40  $\mu\text{m}$  long in type species. Lateral field with two ridges or three to four incisures, inner ones close together. **Cephalic region conoid, continuous with body, smooth.** **Second-stage juvenile:** Body 0.61–0.91 mm and stylet 14–17  $\mu\text{m}$  long in type species. **Lateral field with three incisures.** Cephalic region conoid-rounded, continuous, smooth. Excretory pore anterior to hemizonid, close to median bulb. Tail elongate-tapering, in type species 77–113  $\mu\text{m}$  long, with a **bulbous tip** bearing a small process, and hyaline portion about one-fourth or less of tail length. Haploid chromosome number = 7 (vs.  $n = 13\text{--}19$  in *Meloidogyne* spp.).

#### Type species

*Spartonema spartinae* (Rau & Fassuliotis, 1965) Siddiqi, 1986

syn. *Hypsoperine spartinae* Rau & Fassuliotis, 1965

*Meloidogyne spartinae* (Rau & Fassuliotis) Whitehead, 1968

*Hypsoperine* (*Spartonema*) *spartinae* Rau & Fassuliotis, 1965 (Siddiqi, 1986)

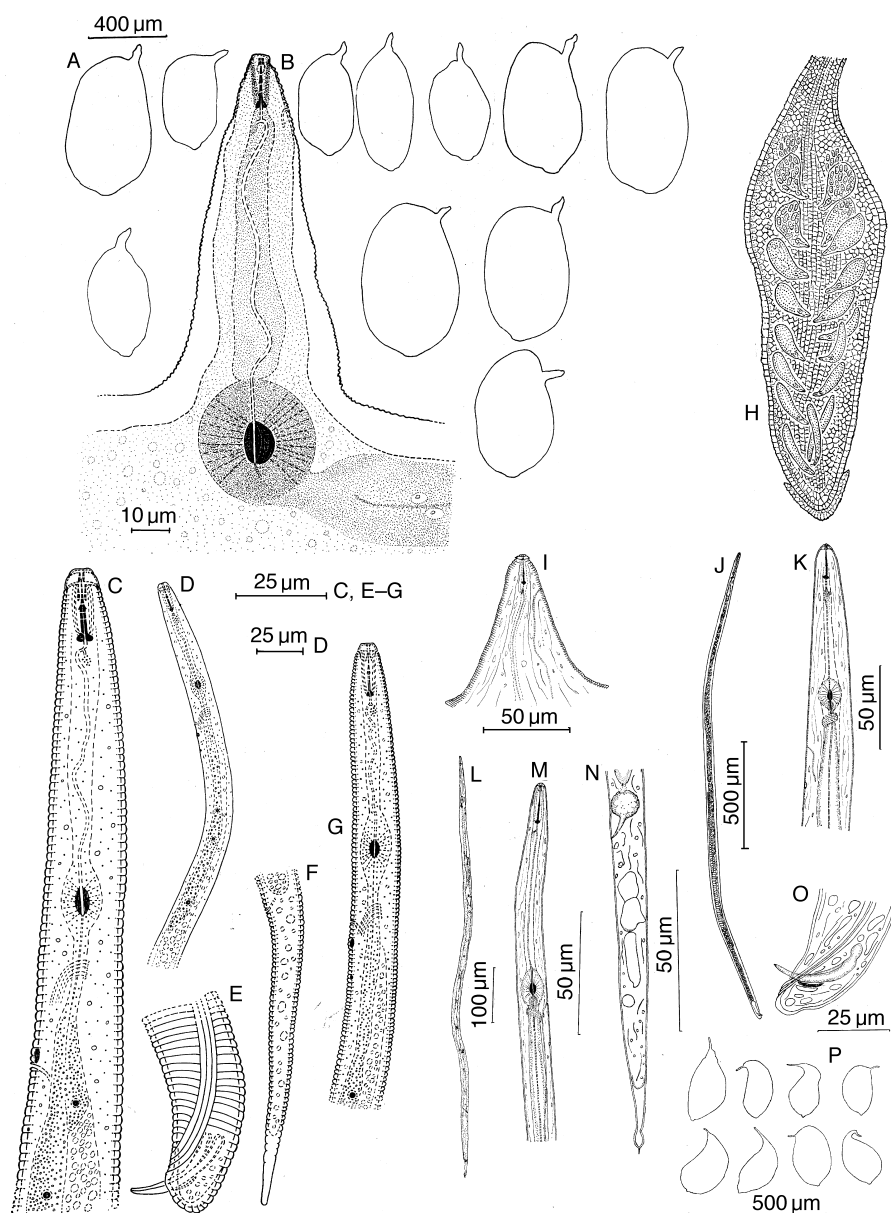
#### Other species

*Spartonema kikuyense* (De Grisse, 1961) comb. n.

syn. *Meloidogyne kikuyensis* De Grisse, 1961

ETYMOLOGY. From Greek *sparton* = a kind of aquatic grass, and also from type species name *spartinae*, and *nema* = nematode.

The type species is a parasite of smooth cordgrass, *Spartina alterniflora* Loiselius in South Carolina and Florida, USA. The feeding position in roots is parallel to the



**Fig. 82.** A–G. *Meloidogyne graminis* (Sledge & Golden). H. *Meloidogyne ottersoni* (Thorne), female in roots of *Phalaris arundinacea* (L.). I–P. *Spartonema spartinae* (Rau & Fassuliotis). A and P. Outlines of females. B and I. Head ends of females. C and K. Anterior ends of males. D, G and M. Anterior ends of second-stage juveniles. E and O. Posterior ends of males. F and N. Tail ends of second-stage juveniles. J. Male. L. Second-stage juvenile. (A–G. After Sledge & Golden (1964). H. Position of feeding nematodes in host. After Thorne (1969). I–P. After Rau & Fassuliotis (1965), courtesy Helminthological Society of Washington.)

root axis with the head directed away from the root apex. During isolation females are easily ruptured due to their thin cuticle.

### **Genus dubium *Meloidoderella* Khan & Husain, 1972**

The genus *Meloidoderella* Khan & Husain, 1972 was regarded by Khan (1972) as morphologically intermediate between *Heterodera* and *Meloidogyne*, sharing equally the characters of both the genera. Husain (1976) and Coomans (1979) proposed the subfamily Meloidoderellinae and the tribe Meloidoderellini, respectively, and discussed their systematic positions. The type and only species of the genus, *Meloidoderella indica* Khan & Husain, 1972 (= *Meloidoderella indica* Khan, 1972) was described from the galled roots of tomato infested by the root-knot nematode near Aligarh, India. It appears that the authors were dealing with a *Meloidogyne* sp. or a mixed population of *Meloidogyne* and a few cysts of *Globodera*. The arguments in favour of the coloration of the female, the position of the excretory pore and the surface pattern of the 'cyst' cuticle are not convincing. These inconsistencies, poor description and the unavailability of the type specimens, either from the authors or from the place of deposition, to several workers led Siddiqi (1986) to consider *Meloidoderella indica* as genus *et species dubia*.

### **Subfamily Nacobboderinae Golden & Jensen, 1974**

**syn. Meloineminae Husain, 1976 (correct spelling Meloinematinae)**

**Nacobboderini Golden & Jensen, 1974 (Coomans, 1979)**

#### **Diagnosis**

Meloidogynidae. Root-gall-inciting. Cephalic region offset, annulated; labial disc indistinct; framework strongly sclerotized, stylet well developed. Oesophageal glands extending over intestine mostly ventrally. **Third- and fourth-stage juveniles vermiform, with a stylet. Preadult female vermiform with two opposed, outstretched immature ovaries and a short tail. Mature female spheroid to pear-shaped, with a long neck; vulva subterminal, at some distance from anus; a short tail present; didelphic-prodelphic with coiled ovaries. No cyst stage. Male develops by metamorphosis in saccate juvenile; tail conoid-rounded, with or without a bursa.**

#### **Type genus**

*Meloinema* Choi & Geraert, 1974

syn. *Nacobbodera* Golden & Jensen, 1974

#### **Other genus**

*Bursadiera* Ivanova & Krall, 1985

### **Key to genera of Nacobboderinae**

1. Excretory pore located opposite anterior margins of median oesophageal bulb or more anteriorly; male tail lacking a bursa ..... *Meloinema*  
Excretory pore located opposite posterior margins of median oesophageal bulb or more posteriorly; male tail with a bursa ..... *Bursadiera*

**Genus *Meloinema* Choi & Geraert, 1974****syn. *Nacobbodera* Golden & Jensen, 1974**

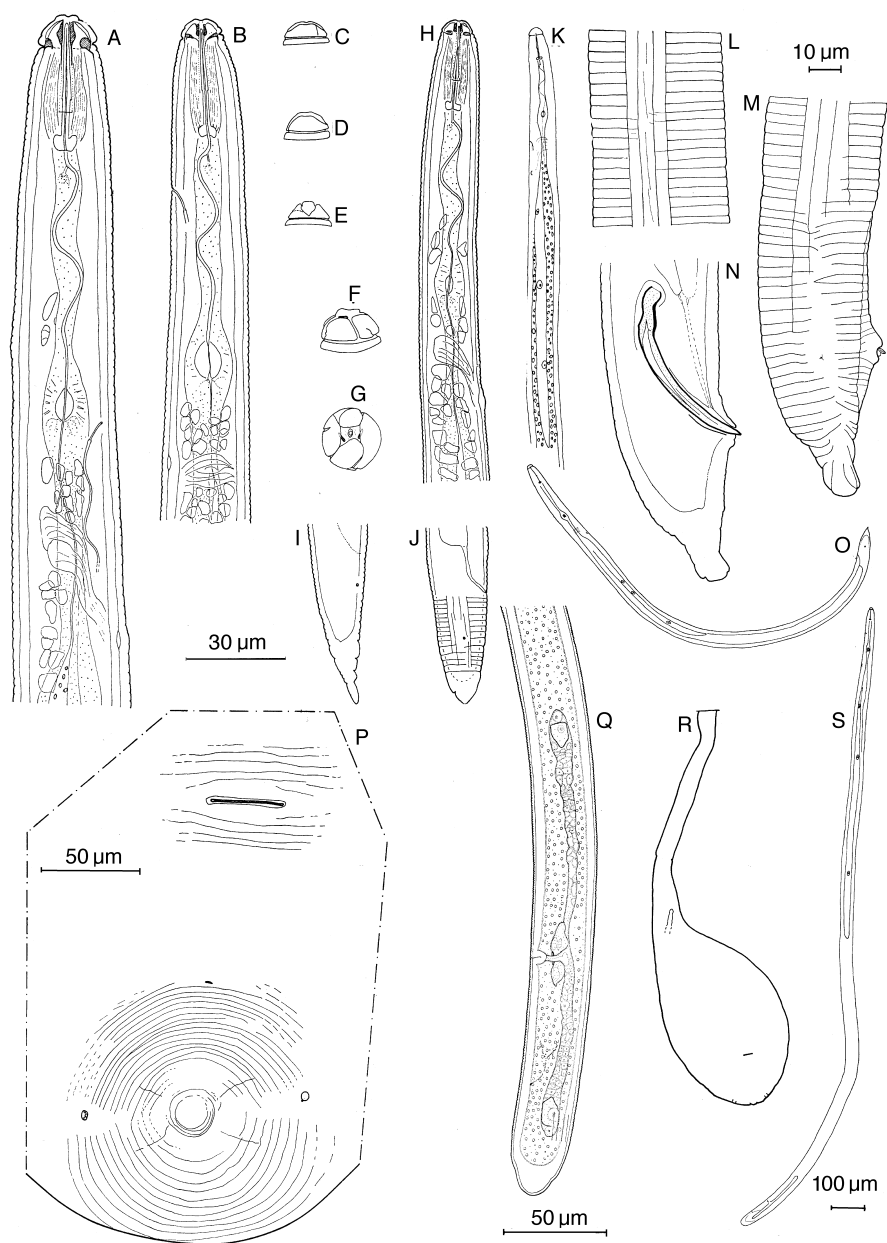
(Fig. 83)

**Diagnosis**

Nacobboderinae. **Preadult female:** Vermiform, slender, 1.3–2.2 mm long. Cuticle distinctly annulated; lateral field with four incisures. Stylet 32–36  $\mu\text{m}$  long in type species, conus longer than shaft. Orifice of dorsal oesophageal gland 4–5  $\mu\text{m}$  behind stylet base. Median bulb oval, with enormous refractive thickenings. **Oesophageal glands in preadult female, male and second-stage juveniles of type species very long, extending to about mid-body, glands mostly on left subventral side of intestine. Excretory pore opposite median bulb or much anterior.** Hemizonid behind nerve ring. Vulva near anus. Didelphic, amphidelphic; ovaries immature. Tail obtusely rounded, one to two anal body widths long. **Mature female:** Pearly white, may become yellow or light brown when old; posterior half swollen, spheroid to pear-shaped, anterior half in the form of a long neck. Cephalic region offset. Stylet about 30–35  $\mu\text{m}$  long in type species. Median bulb with large refractive thickenings; excretory pore just anterior to it. **Vulva a transverse slit, 50–122  $\mu\text{m}$  from anus. A short stumpy tail present.** Phasmids large, conspicuous, halfway between tail tip and anus. **Male:** Vermiform; 1.7–2.9 mm long with 34–40  $\mu\text{m}$  long stylet, 50–64  $\mu\text{m}$  long spicules and 13–17  $\mu\text{m}$  long gubernaculum. **Lateral field with four to five incisures.** Cephalic region offset with three to four annules and strongly sclerotized framework. Excretory pore behind middle of median bulb. Median bulb oval, with refractive thickenings of medium strength. Oesophageal glands extending over intestine ventrally and mostly sublaterally. Testis single, outstretched. Spicules cephalated, slender distally. Gubernaculum well developed, fixed. Bursa absent. Tail short, conoid, with rounded tip, 1–1.7 times anal body width long; tail end twisted. **Second-stage juvenile:** Vermiform, 0.52–0.75 mm long with 23–29  $\mu\text{m}$  long stylet in type species. Lateral field with four incisures, not areolated. Cephalic region offset, annulated; labial disc indistinct, sclerotization strong. Tail conical, two to three times anal body width long, with a large terminal hyaline portion; phasmids anterior to middle of tail.

**Type species***Meloinema kerongense* Choi & Geraert, 1974**Other species***Meloinema chitwoodi* (Golden & Jensen, 1974) Stone, 1978syn. *Nacobbodera chitwoodi* Golden & Jensen, 1974*Meloinema maritimum* Eroshenko, 1990*Meloinema silvicolium* Kleynhans, 1988**Remarks**

*Nacobbodera* Golden & Jensen, 1974 was synonymized with *Meloinema* Choi & Geraert, 1974 by Stone (1978). Ivanova & Krall (1985) regarded *Nacobbodera* as undoubtedly synonymous with *Meloinema*. Luc *et al.* (1988), however, differentiated *Nacobbodera* from *Meloinema* on two points: (i) relatively short oesophageal gland



**Fig. 83.** *Meloinema kerongense* Choi and Geraert. A, B and H. Anterior regions of male, female and juvenile, respectively. C–E. Surface views of female heads; E. median, C and D lateral views. F and G. Surface and *en face* views, respectively of male head. I and J. Tail ends of juvenile. K. Oesophageal region of male. L. Lateral field at midbody region of male. M and N. Tail ends of male. O. Second-stage juvenile. P. Surface view of tail tip and vulval region, showing cuticular striation, vulva, anus and phasmids. Q and S. Immature females. R. Swollen body of mature female. (After Choi and Geraert (1974), courtesy *Nematologica*.)



overlap; and (ii) excretory pore located anterior to the level of median bulb in female and second-stage juveniles and posterior to isthmus in males as compared to anterior position (half a stylet length behind basal knobs) in female and at level of metacarpus in male of *Meloinema*. *Meloinema silvicolum* Kleyhans, 1988 was described as having a relatively long overlap of the oesophagus in the male but with the excretory pore in all stages being located behind the median bulb. Thus the character of the position of the excretory pore is variable in this group and the sole character of the relative length of the oesophageal glands needs further study as glands are sometimes difficult to differentiate from adjoining tissues. There seem to be insufficient differences to distinguish between the two genera.

ETYMOLOGY. Greek *mélon* = apple, and *nema* for nematode.

The type species parasitizes roots of *Syringa oblata* Lindl, Kerong Mt in Chung Nam Province, Korea. The anterior slender part of the mature female remains buried in the root with the head reaching the stele, while the posterior swollen part protrudes. Eggs are laid in a gelatinous matrix within which a few males may be found. *Meloinema chitwoodi* was found parasitizing roots of Douglas fir (*Pseudotsuga menziesii*) in Oregon, USA. The nematodes appeared to be embedded in the mycorrhizae coating the roots, but their heads extended deep into the roots (Golden & Jensen, 1974). *Meloinema silvicolum* occurred in forest soil in South Africa.

### Genus *Bursadera* Ivanova & Krall, 1985

(Fig. 84)

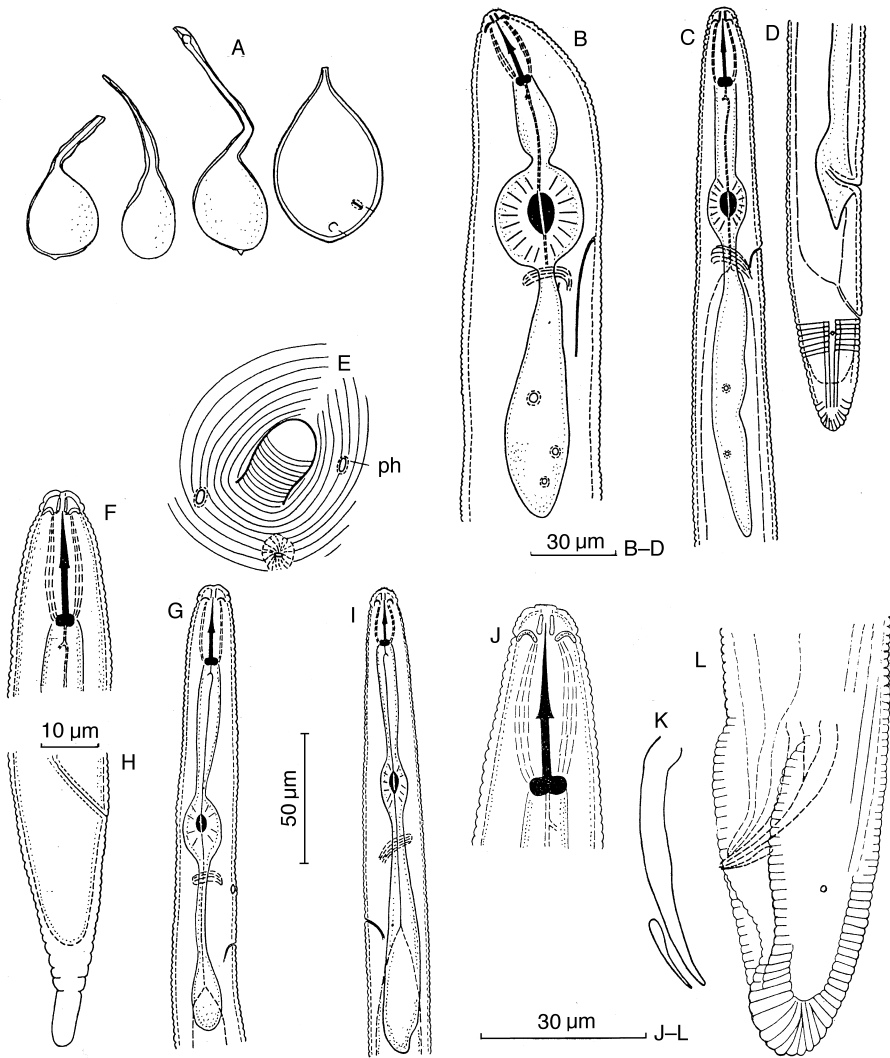
#### Diagnosis

Nacobboderinae. Cephalic region rounded, with two to three annules and a labial disc, offset from body by a constriction; cephalic framework strongly sclerotized. Stylet in females 29–30  $\mu\text{m}$  and in males 29–32  $\mu\text{m}$  long. Excretory pore at or posterior to median oesophageal bulb in all stages. Oesophageal glands forming a short lobe over intestine. Immature female vermiform, with far posterior vulva at about 92% of body length. Mature female with a long slender neck and spheroidal body with vulva and anus lying in the posterior region; **a minutely rounded tail projection present; a transverse vulva separated from pore-like anus by twice the distance between tail tip and anus.** Distinct lens-like phasmids present near anus level. A perineal pattern as in *Meloidogyne* absent but striae make a circular pattern around the tail projection. Male body 1.935–2.251 mm long;  $a = 37\text{--}56$  in type species. **Male tail 1–1.5 anal body width long**, obtusely rounded and annulated. **Bursa distinct**, arising anterior to spicules and extending to tail terminus. Spicules cephalated, distally pointed, slightly arcuate ventrally, 46–49  $\mu\text{m}$  long. Gubernaculum linear. Phasmids pore-like, adanal or just postanal in female and male. Second-stage juveniles with 0.534–0.599 mm long body,  $a = 21.6\text{--}24.9$ , stylet 21.6–22.5  $\mu\text{m}$  long and conoid tail with distinct hyaline region (about two-fifths of tail length) and a minutely rounded terminus, in type species.

#### Type species

*Bursadera longicollum* Ivanova & Krall, 1985

No other species.



**Fig. 84.** *Bursadera longicollum* Ivanova & Krall. A. Females. B. Head end of female. C. Oesophageal region of immature female. D. Posterior region of immature female. E. Tail end of mature female showing phasmids (ph). F and G. Anterior ends of second-stage juvenile. H. Tail end of second-stage juvenile. I and J. Anterior regions of male. K. Spicule and gubernaculum. L. Tail end showing bursa and phasmid. (After Ivanova & Krall, 1985.)

**ETYMOLOGY.** From *bursa*, and Greek *deras* = skin, modified to the Latin feminine, as for *Heterodera*.

The type species parasitizes roots of willow tree, *Salix kirilowiana*, in eastern Tien Shan, Kirghizia.

## FAMILY HETERODERIDAE

### (Cyst and cystoid nematodes)

As the most highly evolved and economically very important plant parasites, the members of this group stand out by their remarkable and efficient parasitic adaptations. The adult female is swollen, sedentary, with most of the body exposed on the root surface while the anterior part of the body is buried in the root abutting the feeding site. The females are globular and white and give a pearly or white bead-like appearance to the root to which they are attached. The feeding site is a syncytium formed by the breakdown of walls between adjacent cells (without nuclear proliferation). The component cells become enlarged, with large vacuoles and densely granular cytoplasm. The syncytium has the characteristics of a transfer cell, with the syncytial surface adjacent to the stele enlarged by the development of numerous, minute wall ingrowths. The development of the syncytium appears to be initiated by substances in secretions from the nematode dorsal oesophageal gland injected through the stylet into host tissues. The feeding mechanism involves formation of complex feeding tubes within the syncytial cytoplasm.

Most of the eggs are generally retained within the swollen body, but in some species one to 200 eggs may be laid in a gelatinous matrix produced through the vulva. In several genera, the female body turns into a hard-walled protective cyst. Normally feeding does not initiate root-galls. The males, although provided with a well-developed stylet and a muscular pump, do not feed. They have enough energy to survive for as long as 10 days for the sole purpose of locating and fertilizing the females. The great majority of species are amphimictic (bisexual), but a few are known to be parthenogenetic (uniparental). However, even the bisexual species are fully capable of reproducing by parthenogenesis.

In many species the second-stage juveniles remain dormant in the eggs until appropriate stimulation is received, following which they hatch. The stimulation may be increased by temperature, hydration or specific chemicals in the exudates of host plant roots. In North India, the harvest of the wheat crop in April is followed by hot summer conditions with temperatures over 20°C when *H. avenae* juveniles enter into a state of dormancy. The cyst dormancy persists in soil temperatures up to 45°C until November when the temperature drops and the new crop is planted. The cysts of *A. avenae* remain viable after 6 months' storage at the ultra-low temperature of -180°C (Dhawan & Rao, 1988).

The eggs and juveniles in the cysts remain viable for a number of years. In adverse conditions or when the food supply is low, the juveniles generally develop into males. In resistant host varieties in which the juveniles are not able to incite giant feeding cells, the development also results in the production of males.

The life cycle from egg to egg stage in *Heterodera* species generally takes 16–32 days; a variation of up to 10 days may occur when situations under which the life cycle is studied differ considerably. In India, *H. oryzae* completes its life cycle on banana in 23 days (Charles & Venkitesan, 1995) and on rice in 30 days (Jayaprakash & Rao, 1982). Second-stage juveniles of *Rhizonema sequoiae* in a glasshouse at 16°C develop to adult females in 6 months and to adult males in 3–4 months; at 18°C the life cycle was completed in 8 months; at 25°C the nematode populations died out in 6 months (Cid del Prado Vera *et al.*, 1984).

These so-called cyst and cystoid (when the cysts are not formed) nematodes are

well adapted to a variety of climatic conditions. Most *Globodera* spp. and some *Heterodera* spp. (*H. carotae*, *H. schachtii*), are adapted to cold climates as their activity is greatest at about 15–20°C and ceases at about 40°C. Accordingly, in the temperate regions and in the tropics, they flourish only at high altitudes or on crops which develop during the winter. On the other hand, several *Heterodera* spp. (e.g. *H. cajani*, *H. moths*, *H. sacchari*, *H. zae*) are found in the tropics and do well at temperatures above 20°C. Eighteen species of cyst nematodes have been reported from India and 23 species occur in the tropics (see hosts and localities in Evans & Rowe (1998)).

Some temperate species require exposure to cold before they can hatch. They use their stylet for puncturing and cutting through the egg-shell. The migratory second-stage juveniles usually penetrate near the growing root tip and move up within the root to take up a feeding position near the pericycle or stele. The nematode, so far, is a migratory endoparasite. After feeding on the root, the nematode grows and becomes obese. It is now a true sedentary endoparasite.

The female ruptures the root tissue so that its posterior is exposed. It is only then that fertilization is possible. Some species of *Heterodera* produce a gelatinous matrix through the vulva that may cover the posterior region. The female produces pheromones in exudates that emanate from the vulva to attract males. The female produces a large number of eggs (up to 500) which are retained in body or, in some cases, up to 200 eggs may be laid in this matrix, which forms an egg-sac. The reason why this matrix is produced in the cyst-forming species is not clear, but it may be an adaptation to producing eggs with different survival strategies. Perhaps in their predecessors it was the sole means of protecting the eggs when the cyst formation had not yet been evolved. *Globodera* spp. produce very little or no gelatinous matrix. The exposed body of the female is sealed onto the root by a brownish 'cement' which appears on mature females before they turn brown to form the cyst (e.g. *Heterodera*, *Globodera*).

Association of cyst nematodes with fungal root pathogens produces disease complexes much more severe than those produced individually by either pathogen. For example, *Heterodera schachtii* with *Rhizoctonia solani* on sugarbeet and *Globodera rostochiensis* with *Verticillium dahliae* on potato interact to produce severe disease complexes. Severe disease complexes of soybean are caused by the involvement of *Heterodera glycines* with pathogenic fungi such as *Rhizoctonia solani*, *Fusarium* spp. and *Pythium* spp. There are several fungi which can infect and kill the cyst nematodes and which can be used as biological control agents against them (Kerry, 1986; Crump, 1987; Saifullah, 1996). *Verticillium chlamydosporium* and *Trichoderma harzianum* infection killed potato cyst nematode females and eggs (Saifullah, 1996; Saifullah & Thomas, 1997). Scanning electron microscopy showed the parasitism of these fungi to cyst nematodes (Lopez-Llorca & Duncan, 1991; Saifullah and Thomas, 1996).

Resistance-breaking pathotypes or biotypes are known to occur in species of *Heterodera* and *Globodera*. The pathotypes are determined on their ability to multiply on defined resistant lines. All pathotypes of *G. rostochiensis* and *G. pallida* possess the innate ability to induce feeding transfer cells in potato roots. The expression of this ability, however, depends on a compatible relationship between the host tissue and the nematode saliva injected into it. Breeding plants for resistance and crop

rotation provide good control measures. Combining these with limited use of chemicals (both soil fumigants and 'systemic' nematicides), after appropriate trials in local soil and climatic conditions, helps in managing populations so that they remain below the economic threshold.

The cyst nematodes show a good deal of host specificity and a highly specialized plant parasitism. There are about 100 nominal species of cyst nematodes belonging to six genera (there are also about a dozen non-cyst-forming heteroderid genera), many of which have co-evolved with their host plants. Their co-evolution with their hosts has been studied by Krall & Krall (1970) and Stone (1979). The former authors noted that the most ancient plant group, the Protanthophyta (Magnoliales, Ranunculales, etc.) are not parasitized by the cyst nematodes, the recent angiosperms (Asterales, Cyperales, Umbellales, etc.) are parasitized with a limited host range, and the intermediate group, the Mesanthophyta (Caryophyllales, Leguminales, Polygonales, Solanales, etc.) are most abundantly parasitized. Stone (1979) examined the host and distribution records of various groups of cyst nematodes and found a pattern of co-evolution. The species of *Globodera*, for example, parasitize Solanaceae in the New World and Compositae only in Europe. He speculates that *Globodera* may have originated in Gondwanaland at the time when angiosperms evolved and became widely dispersed there in the Mesozoic. Evans & Rowe (1998) list the main host plant families of various species of cyst-forming heteroderids and state that they, in general, have hosts within particular plant species, e.g. *Cactodera* are found on members of the Cactaceae, Amaranthaceae and Chenopodiaceae, *Cactodera betulae* is found normally on birch, occasionally on alder, and species of *Heterodera* and *Punctodera* attack members of the Poaceae. *Globodera* spp. seem to have co-evolved with members of the Solanaceae.

Meagher (1977) suggested that *Heterodera avenae* originated in Europe from where it was distributed to other parts of the world largely by the activity of man, but also by wind movement of cysts. He stated that the dissemination of *H. avenae* throughout the Old World would have commenced about 4000 BC, during the Neolithic Revolution when man began farming wheat and barley. However, the parasitism of grasses by this nematode suggests that its distribution in the Old World must have occurred much earlier than the Neolithic Revolution.

The chickpea cyst nematode, *H. ciceri*, may cause 20% loss to chickpea in northern Syria. It also attacks lentils and peas. *Heterodera swarupi* is yet another parasite of chickpea reported from India (Sharma *et al.*, 1999). *Heterodera glycines*, the soybean cyst nematode, appears to have originated in China and from there it was dispersed to Japan, the USA and other parts of the world. Liu *et al.* (1997) stated that soybean originated in China and was domesticated about 3500 BC and that soybean seeds found in an ancient (circa 300 years BC) tomb in Shanxi Province suggested that the centre of origin of soybean was in China. It is widely distributed in various provinces of China (Liu *et al.*, 1997).

*Meloidodera* spp., the cystoid nematodes, induce single uninucleate giant cell (vs. multinucleate syncytia by heteroderids) by feeding in the pericycle. The wall of the giant cell thickens and the modified mitochondria, plastids and endoplasmic reticulum are similar to those of the giant cells induced by the Heteroderidae (Mundo-Ocampo & Baldwin, 1983). *Meloidodera mexicana* and *M. charis* parasitize agricultural crops; their feeding induces giant cell formation in the parenchyma of

the vascular cylinder, causing severe distortion of the vascular tissue in chilli and tejocote tree (Cid del Prado & Cárdenas, 1995) and in *Peonica californica* and *Artemisia tridentata* (Inserra & Vovlas, 1986). *Meloidodera mexicana* attacks chilli, beans, pumpkin, tomato and maize, and reduces significantly chilli plant growth and fruit yield (Fuentes *et al.*, 1997).

The identification of the genera and species of the Heteroderidae is largely based on the morphology of the female, cyst and second-stage juveniles. The cyst **cone** or **vulval basin** (when a cone is not formed) and the perineal characteristics are very important in the generic and species identifications (Cooper, 1955; Mulvey, 1960, 1972; Hesling, 1978, etc.). The position of the anus in respect to the vulva is used for generic differentiation. The surface of the perineum shows ridges and furrows forming two basic patterns (Hesling, 1978): (i) a reticulate or maze-like pattern usually found when the perineal length (distance between vulva and anus) exceeds 60  $\mu\text{m}$ ; and (ii) a pattern of roughly parallel ridges usually found when the perineal length is less than 50  $\mu\text{m}$ . The number and relative breadths of the perineal ridges or grooves have been used in species identification (Miller & Gray, 1972). Near the vulval lips or the edges of the vulval fenestrae, there are in several species round to oval protuberances or **vulval papillae** (Green, 1975), which are mainly modifications of the ridge and furrow pattern (Mulvey, 1973). These are sometimes used in identification. The **Granek's ratio** (distance from the anus to the nearest edge of the fenestra divided by the length of the fenestra) is also helpful in species identification.

The **vulval slit** length and the translucent area around it, called the **fenestra**, are also important in species differentiation. The vulva may be carried on a band of thickened tissue, the **vulval bridge**. The translucent area is composed of much thinner layers of tissue which, with the vulva, are lost in older cysts and form escape exits for the juveniles. If two thin-walled areas or holes are present one on each side of the vulval bridge, the condition is called **ambifenestrate** (when the fenestrae abut the vulval bridge) or **bifenestrate** (fenestrae well separated and more or less circular). A single thin-walled region or hole, without the vulva supported on a bridge of tissue, is termed **circumfenestrate**. The genus *Bidera* Krall & Krall, 1978, principally based on the bifenestrate condition of the cyst and a short vulval slit, has not met with general acceptance. However, the shape and size of the fenestrae vary between species and provide useful guides for identification. The presence of an extra fenestra under the anus (**anal fenestra**) is a major characteristic of the genus *Punctodera*.

The remnants of tissues and muscles of the vaginal wall lying underneath the fenestral tissue also serve as useful diagnostic features. The vaginal remnant, known as the **sheaf-like organ**, is attached to the cyst wall by two arms running across the vulval cone and called the **underbridge**. The well-developed underbridge is generally associated with prominent bullae (e.g. *H. avenae*, *H. schachtii*). It is lacking in the genera *Globodera*, *Cactodera*, *Punctodera* and *Dolichodera*. Associated with the ends (often branched) of the underbridge are knob-like structures, the **bullae** (Cooper, 1955) which are perhaps the remnants of the muscles. *Heterodera zae* has characteristic of four finger-like bullae arranged as a cross. In some cyst-forming species, adult females and newly formed cysts may be surrounded by a thick, chalky, crazed deposit called the **subcrystalline layer**.

*Heterodera glycines* and *H. schachtii* are very similar but each occupies a different host and geographical distribution. Bakker and Bouwman-Smits (1988) found that

there was considerable difference between the proteins/polypeptides of the two species (as revealed by 2-D PAGE analysis), which had accumulated over millions of years without marked changes in their morphological characters. The two species are also close to *H. trifolii*. Ferris (1994) found ribosomal DNA spacer sequence data of these three species to be nearly identical.

The family name Heteroderidae is attributed to Filipjev (1934) but Wouts & Weischer (1974) concluded that the subfamily name Heteroderinae was first used by Filipjev & Schuurmans Stekhoven (1941) and, under Article 13 of the International Code of Zoological Nomenclature, was made available only by Skarbilovich (1947). However, Wouts *et al.* (1977) reported that Filipjev & Schuurmans Stekhoven (1941), in a key, had separated Heteroderinae from other subfamilies of the Tylenchidae, fulfilling the requirements of the said article and hence they should be regarded as the authorities of the name Heteroderinae.

Chitwood in Chitwood & Chitwood (1950) considered the subfamilies Heteroderinae, Hoplolaiminae and Nacobbinae under Heteroderidae and Skarbilovich (1959) included Heteroderinae, Meloidogyninae, Nacobbinae, Sphaeronematinae and Tylenchulinae under this family. Paramonov (1967) and Wouts & Sher (1971) recognized only Heteroderinae and Meloidogyninae under it; Meloidogyninae was separated from Heteroderinae and raised to family by Wouts (1973). Golden (1971) raised the family Heteroderidae to superfamily, recognizing two families, Heteroderidae and Nacobbidae, under it. Heteroderidae *sensu* Golden (1971) comprised Heteroderinae, Meloidoderinae and Meloidogyninae. Stone (1978) upheld the superfamily Heteroderoidea for Heteroderidae and Meloidogynidae.

Wouts & Sher (1971) redefined Heteroderidae and distinguished three groups of genera in the Heteroderinae (now Heteroderidae). A group characterized by the annulated cuticle of the female included *Meloidodera* and *Cryphodera*. The other two groups with non-annulated female cuticle included cyst-forming *Heterodera* and non-cyst-forming *Atalodera*. On this basis, Wouts (1973) recognized three subfamilies under Heteroderidae: Heteroderinae, Meloidoderinae and Ataloderinae. Coomans (1979) subdivided Meloidoderinae into two tribes: Meloidoderini (plesiomorphic group with equatorial vulva) and Cryphoderini (apomorphic group with a terminal or subterminal vulva), and Heteroderinae also into two tribes, Heteroderini (apomorphic group with terminal or subterminal vulva) and Ataloderini (plesiomorphic group with no cyst stage). Luc *et al.* (1978) argued against recognizing any subdivisions of the family Heteroderidae because the genus *Hylonema* was shown to share characteristics of the subfamilies Ataloderinae, Heteroderinae and Meloidoderinae and subsequently no logical subfamilial structure could be devised.

Wouts & Sher (1971), Stone (1975), Husain (1976) and Hesling (1978) discussed the phylogeny of the heteroderid genera, which were generally supposed to have evolved from present-day Hoplolaimidae. The cephalic regions of male *Meloidodera* and *Cryphodera* are tiled as in some Hoplolaiminae. The *Meloidodera* female has a swollen body but a subequatorial vulva. Luc *et al.* (1978) illustrated an abnormal female of *Hylonema ivorense* which has a non-swollen caudal end resembling that of a hoplolaimid female (Fig. 93, O). Some heteroderid juveniles have a lens-like structure underneath the cuticle, which may be a homologue of the scutellum of the Hoplolaiminae. The first-stage juvenile of *Hoplolaimus concaudajuvencus*

has a conical tail resembling those of heteroderid juveniles. All these similarities point to the likely derivation of the Heteroderidae from a Hoplolaimidae-type ancestor.

Stone (1975) provided a phylogenetic tree for the genera of Heteroderidae based on the head morphology of second-stage juveniles as revealed by SEM and in 1979 published a modified phylogeny for cyst nematodes on the basis of phylogenetic relationships of host plant families as well as nematode morphology. Hesling (1978) gave a modified version of this tree. From *Meloidodera*, two lines are suggested; one leading to *Cryphodera* and *Zelandodera*, the other leading to *Atalodera*, *Globodera*, *Cactodera* and *Heterodera* in that ascending order. *Sarisodera* and *Punctodera* are shown to arise as an independent line from *Atalodera*. The genus *Heterodera* is heterogeneous at present and it may be possible to revalidate *Bidera* which is currently considered as synonymous with it. The genera *Ephippiodera* and *Bidera* are, however, very close to *Heterodera* both phenetically and phylogenetically and are here considered as junior synonyms of *Heterodera*.

Krall & Krall (1978) proposed a modified taxonomy of Heteroderidae based on trophic specialization and co-evolution with host, and proposed the new genera *Bidera* for the *H. avenae* group (which is characterized by a short vulva and the bifenestrate condition of the cyst fenestration) and *Cactodera* for the *H. cacti* group. *Bidera* included *B. avenae*, *B. bifenestra*, *B. hordecalis*, *B. iri*, *B. longicaudata*, *B. mani* and *B. turcomanica*. Mulvey and Golden (1983) synonymized *Bidera* with *Heterodera*. Stone (1986), Siddiqi (1986), Luc *et al.* (1988), etc. did not recognize the genus *Bidera*.

Luc *et al.* (1978) did not recognize any subfamilies under Heteroderidae. Luc *et al.* (1988) upheld the view that heteroderids and meloidogynids belong to a single family, Heteroderidae, whose genera they classified under three subfamilies – Heteroderinae, Meloidogyninae (with *Meloidogyne*) and Nacobboderinae (with *Nacobbodera*, *Meloinema* and *Bursadiera*). Listing of all the heteroderid genera under one subfamily Heteroderinae shows that the authors ignored the phylogenetic concept in classification which was developed by Husain (1976), Coomans (1979), Ferris (1979) and Wouts (1985). Such extreme conservatism apparently avoids solving the problems of proper character analysis and building a sound classification which should reflect phylogeny and have predictive value. Wouts (1985) wrote: 'In order to express genealogical relationships through sister groups within the family Heteroderidae, it is essential that primitive and derived characters are distinguished. For groups that are phylogenetically distant this is easy, but it becomes increasingly difficult when such groups become more closely related.'

Monophyly of *Globodera*, *Cactodera* and *Punctodera* is supported by the characters of the small labial disc of the second-stage juveniles and fused lips in males (Othman *et al.*, 1988) (see also Chapter II for the phylogeny of Heteroderidae). In his phylogenetic analysis using derived characters (synapomorphies) which developed in their immediate ancestor, Wouts (1985) recognized the following six subfamilies under Heteroderidae:

1. Verutinae (large vulval slit).
2. Meloidoderinae (vulval slit > 30 µm long; male body twisted in posterior region).
3. Cryphoderinae (terminal vulva, vulval lips small, anal protuberance).
4. Heteroderinae (loss of annulation, cyst and vulval cone formed, fenestration along vulval slit, lip flap of infective juvenile in *Hylonema*, short vulval slit in *Bidera*).
5. Ataloderinae (D-layer in cuticle, vulva close to anus, narrow glands in juveniles,



anus on inside of vulval lip in *Sherodera*, cyst formation in *Sarisodera*, protruding anus in *Bellodera*).

6. Punctoderinae (fenestration around vulva and anus in *Punctodera*, short vulval slit, protruding vulval area in *Cactodera* and modification around vulva in *Globodera*).

Baldwin *et al.* (1989) suggested the monophyly of ataloderines: *Atalodera*, *Sherodera* and *Thecavermiculatus*. This group is characterized by hatching and retaining second-stage juveniles ( $J_2$ ) in the female body,  $J_2$  with elongate labial disc and fusion of lateral lips with the labial disc and inducing syncytia without wall ingrowths. They also suggested that *Hylonema* belonged to another monophyletic group with *Sarisodera*, *Rhizonema* and *Bellodera*. These genera share narrow submedian lips in  $J_2$  and lack the syncytial host response of ataloderines and heteroderines.

Baldwin & Schouest (1990) gave a revised classification of Heteroderinae *sensu* Luc *et al.* (1988) based on comparative detailed morphology and PAUP (phylogenetic analysis using parsimony). They recognized the following tribes under Heteroderinae: Heteroderini, Verutini Esser, 1981, Meloidoderini Golden, 1971, Cryphoderini Coomans, 1979, Sarisoderini Husain, 1976 and Ataloderini Wouts, 1973 (also see Chapter II, under Cladism).

Baldwin & Schouest's (1990) analyses strongly supported monophyly of all cyst-forming genera (tribe Heteroderini), rejecting the hypothesis of repeated evolution of the cyst stage. Monophyly of Heteroderini with Ataloderini was demonstrated. Monophyly of *Cactodera* with *Heterodera* and *Afenestrata* was indicated, as was the monophyly of ataloderines. Since the cyst stage evolved once in Heteroderinae, the monophyly of ataloderines and other cyst-forming genera was indicated. Their new tribe, Sarisoderini, with *Sarisodera* + *Rhizonema* + *Bellodera* + *Hylonema* and *Ekphymatodera* also indicated monophyly; the synapomorphy of the character of the reduced width of the submedian lips of second-stage juveniles and males strongly supported this monophyly. They stated that *Hylonema* + *Ekphymatodera* were monophyletic and might represent a separate tribe, Hylonemini. *Meloidodera* and *Cryphodera* were considered as relatively ancestral and *Verutus* as typically an out-group. They pointed out that Siddiqi (1986) had removed *Verutus* from the Heteroderidae and placed it in the Rotylenchulidae, and emphasized that *Verutus* was an enigma among the Heteroderinae. Here *Verutus* is classified with *Bilobodera* under Verutinae which is assigned to the Rotylenchulidae.

Baldwin (1986) had hoped for a consensus of certain broad aspects of competing phylogenies of Heteroderidae after repeated analyses of relationships. From the various schemes of classification proposed for Heteroderidae, it is proposed here to recognize three subfamilies – Heteroderinae, Ataloderinae and Meloidoderinae.

A new suborder Heteroderata was proposed by Skarbilovich (1957, as published in 1959) and this is recognized here as the suborder Hoplolaimina Chizhov & Berezina but with a larger composition. Heteroderids are considered here representing a family of Hoplolaimoidea.

**Family Heteroderidae Filipjev & Schuurmans Stekhoven, 1941  
(Skarbilovich, 1947)****syn. Heteroderidae Thorne, 1949****Ataloderidae Wouts, 1973 (Krall & Krall, 1978)****Meloidoderidae Golden, 1971 (Krall & Krall, 1978)****Diagnosis**

Hoplolaimoidea. **Marked sexual dimorphism present.** Cuticle strongly annulated, annules usually modified to form a lace-like pattern on swollen females and cysts. Lateral field with two to four incisures. Cephalic region large, annulated; **labial disc distinct or indistinct, rounded**; basal annule may be indented longitudinally; cephalic framework strongly sclerotized, secondarily reduced in females; **lateral sectors equal to or narrower than submedians.** **Stylet robust, usually over 20  $\mu\text{m}$  long,** with conus about half its total length and prominent basal knobs. Orifice of dorsal oesophageal gland close to stylet base. Median oesophageal bulb ovoid to rounded, with prominent refractive thickenings. **Oesophageal glands elongated, extending over intestine mostly ventrally,** but also laterally; subventral glands asymmetrical, longer than dorsal gland, SVN always behind DN. **Female:** Sedentary, swollen, elongate-oval, oval, lemon-shaped or spheroidal, with a short neck, may or may not form cyst. No preadult vermiform stage. Cuticle thick. Vulva equatorial to usually terminal. Tail absent; **anus dorsally subterminal or terminal.** Cuticle abnormally thickened, with annulation or surface variously patterned; **perineum lacking finger-print-like pattern.** **Excretory pore** in anterior region but also **opposite or usually posterior to valve of median bulb.** **Stylet over 17  $\mu\text{m}$  long.** **Male:** Vermiform, develops through metamorphosis within a swollen juvenile (except in *Meloidodera*). Cuticle thick, annulated. Lateral fields with three or four incisures, outer bands may be areolated. Cephalic region regularly annulated, offset or continuous, labial disc distinct or indistinct, rounded; framework strongly sclerotized. Stylet robust, 20–46  $\mu\text{m}$  long, with prominent knobs. Oesophagus well developed. Testis single, anteriorly outstretched. Tail less than one anal body width long, bluntly rounded, hemispherical, or absent; tail end twisted. **Bursa absent.** Phasmids near cloacal aperture. **Second-stage juvenile:** Infective stage that emerges out of egg. Body slender, vermiform, straight to arcuate on death. Stylet robust, over 17  $\mu\text{m}$  long; tail conical, with pronounced hyaline terminal portion; phasmids anterior to middle of tail. **Third- and fourth-stage juveniles swollen, with robust stylet.** Obligate parasites of plant roots.

**Type subfamily**

Heteroderinae Filipjev &amp; Schuurmans Stekhoven, 1941

**Other subfamilies**

Meloidoderinae Golden, 1971

Ataloderinae Wouts, 1973

**Key to subfamilies of Heteroderidae**

1. Vulva equatorial; male development not through metamorphosis ..... **Meloidoderinae**  
     Vulva terminal or subterminal; male development through metamorphosis..... **2**
2. Female turns into a hard-walled cyst ..... **Heteroderinae**  
     Female does not turn into a hard-walled cyst ..... **Ataloderinae**

**Subfamily Heteroderinae Filipjev & Schuurmans Stekhoven, 1941****syn. Heteroderini Filipjev & Schuurmans Stekhoven (Coomans, 1979)****Punctoderinae Krall & Krall, 1978****Sarisoderinae Husain, 1976 (also proposed by Krall & Krall, 1978)****Diagnosis**

Heteroderidae. Mature female spherical, pear or lemon-shaped with a short neck, **turns into a tough, hard-walled, yellowish, light to dark brown or black cyst** containing eggs and juveniles, some eggs may be laid in a gelatinous matrix. **Cuticle surface with a zig-zag or lace-like pattern; annulation absent on mature female and cyst.** Vulva and anus close together, almost terminal, on a raised vulval cone or in a flat to concave vulval basin. Clear hyaline vulval fenestra(e) present; an anal fenestra present only in *Punctodera*. Male develops through metamorphosis, has an annulated cephalic region, four incisures in lateral field and an extremely short hemispherical tail, rarely tail absent (*Sarisodera*). Bursa absent. Second-stage juveniles with four incisures (three incisures in *Dolichodera*) in each lateral field.

**Type genus***Heterodera* Schmidt, 1871**Other genera:**

*Afenestrata* Baldwin & Bell, 1985  
*Cactodera* Krall & Krall, 1978  
*Dolichodera* Mulvey & Ebsary, 1980  
*Globodera* Skarbilovich, 1959  
*Punctodera* Mulvey & Stone, 1976

**Note**

*Heteroderoides* Kirjanova, 1959 is an unavailable generic name because a type species was not designated.

**Key to genera of Heteroderinae**

1. Vulval fenestration absent ..... ***Afenestrata***  
     Vulval fenestration present ..... **2**
2. Body with a terminal cone ..... **3**  
     Body without a terminal cone ..... **4**
3. Cuticular surface with roughly parallel ridges; vulval denticles present;  
     circumfenestrate ..... ***Cactodera***

- Cuticular surface with lace-like or zig-zag ridges; vulval denticles generally absent; rarely circumfenestrate ..... *Heterodera*
4. Anal region with fenestration ..... *Punctodera*  
 Anal region without fenestration ..... 5
5. Mature female and cyst spheroidal; perineal tubercles present; bullae usually absent ..... *Globodera*  
 Mature female and cyst elongate-oval; perineal tubercles absent; bullae present ..... *Dolichodera*

### Genus *Heterodera* Schmidt, 1871

syn. *Tylenchus* (*Heterodera* Schmidt, 1871)

*Heterodera* (*Heterodera*) Schmidt, 1871

*Heterobolbus* Railliet, 1896 (= junior objective synonym)

*Bidera* Krall & Krall, 1978

(*Bidera* in Krall & Krall, 1973 = nomen nudum)

*Ephippiodera* Shagalina & Krall, 1981

(Fig. 85; 86, A, C–H; 87, Q–Z)

### Diagnosis

Heteroderinae. **Mature female and cyst:** Lemon-shaped with a short neck and **terminal cone**, turns into a hard-walled cyst, brown to black in colour, **with a lace-like or zig-zag pattern**. D-layer in cuticle rudimentary or absent; subcrystalline layer present or absent. Vulva terminal; slit 10–60 µm long. Anus dorsally subterminal, near vulva but not on vulval lip. Vulval fenestration present, **ambifenestrate**, **bifenestrate** or very rarely circumfenestrate; **anal fenestration absent**. Vaginal remnant, underbridge and bullae often present. Most eggs retained in body, but some laid in a gelatinous matrix. **Male:** Lateral fields each with four incisures, outer band often areolated. Cephalic region generally offset by a constriction, and with three to six annules; labial disc indistinct; basal lip annule may or may not be indented. Tail end twisted. Spicules robust, over 30 µm long, with blunt bifid or single tip. **Second-stage juvenile:** Body slender, straight to arcuate. Cephalic region generally continuous; labial disc indistinct; in SEM, disc elongate oval. Stylet less than 30 µm long. Oesophageal glands filling body cavity width. Tail with prominent terminal hyaline part. Phasmids punctiform, without a lens-like structure underneath in muscle layer. **Feeding induces a syncytium.**

### Type species

*Heterodera schachtii* A. Schmidt, 1871

syn. *Tylenchus schachtii* (Schmidt) Örley, 1880

*Heterodera schachtii minor* O. Schmidt, 1930

### Other species

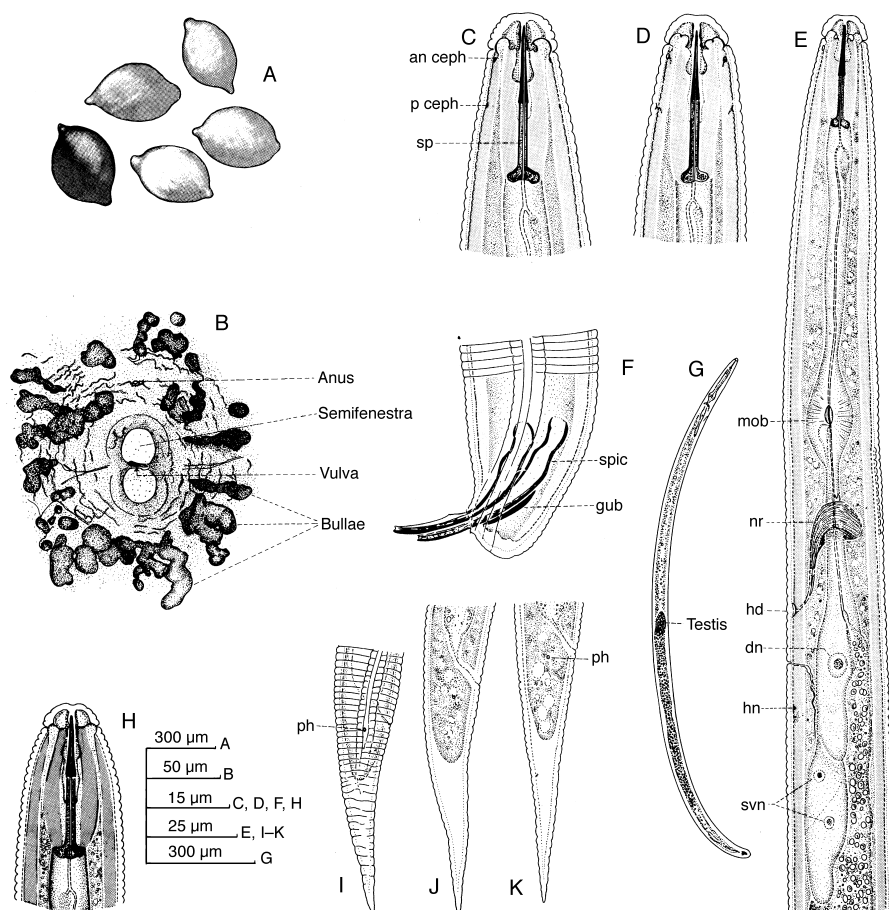
*Heterodera amygdali* Kirjanova & Ivanova, 1975

*H. arenaria* Cooper, 1955

syn. *Bidera arenaria* (Cooper) Krall & Krall, 1978

*H. aucklandica* Wouts & Sturhan, 1995

*H. avenae* Wollenweber, 1924



**Fig. 85.** *Heterodera avenae* Wollenweber. From oats at Woburn, England. A. Cysts. B. En face view of vulval cone of cyst. C and D. Head ends of male. E. Oesophageal region of male. F. Tail end of male. G. Male. H and I-K. Head end and tail ends of second-stage juveniles, respectively. an ceph., anterior cephalid; dn, dorsal gland nucleus; gub, gubernaculum; hd, hemazonid; hn, hemizonion; mob, median oesophageal bulb; nr, nerve ring; p ceph., posterior cephalid; ph, phasmid; sp, spear; spic, spicule; svn, subventral gland nuclei. (After Williams and Siddiqi (1972): *CIH Descriptions of Plant-parasitic Nematodes*.)

syn. *Heterodera schachtii* var. *avenae* Wollenweber, 1924

*Bidera avenae* (Wollenweber) Krall & Krall, 1978

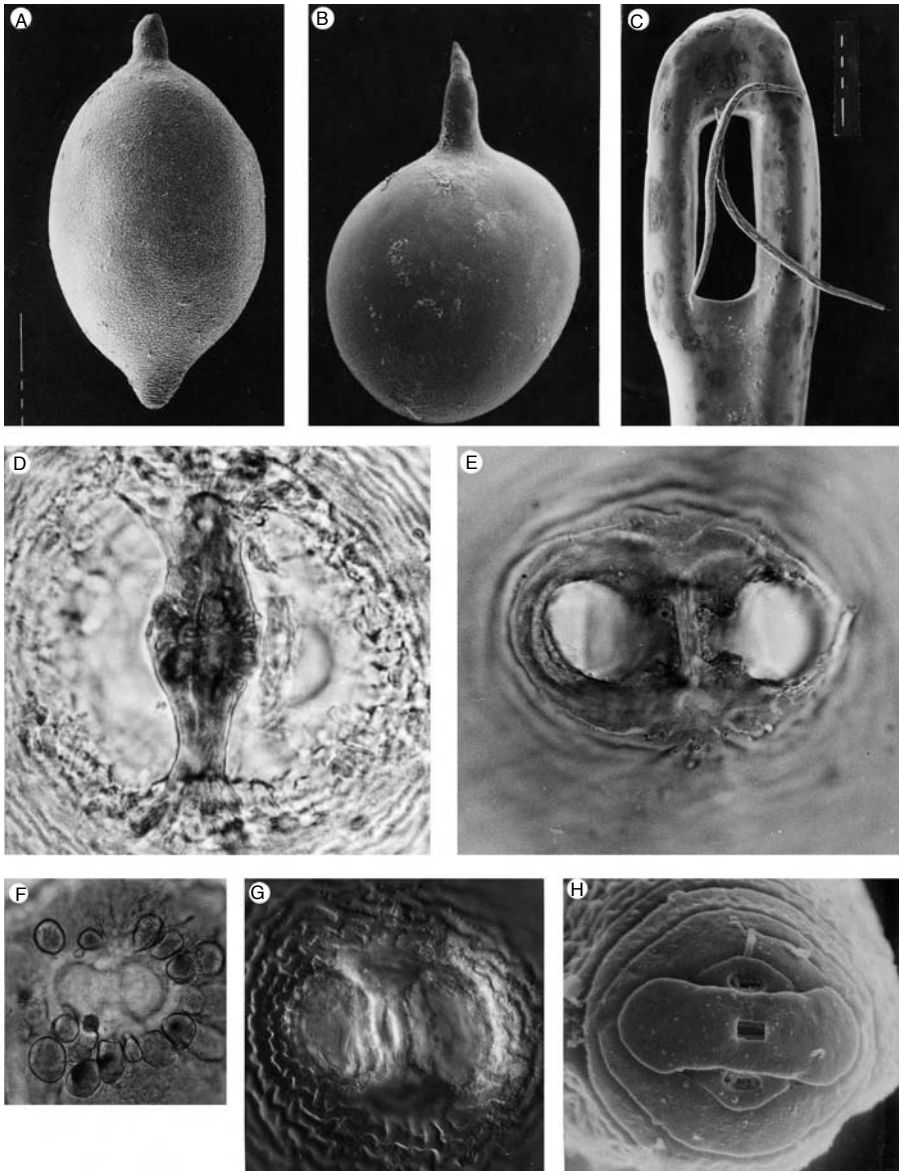
*Heterodera schachtii* major O. Schmidt, 1930

*Heterodera maior* O. Schmidt, 1930

*Heterodera ustinovi* Kirjanova, 1969

*Bidera ustinovi* (Kirjanova) Krall & Krall, 1978

*H. bergeniae* Maqbool & Shahina, 1988



**Fig. 86.** A. *Heterodera avenae* Wollenweber, cyst (longest line = 100  $\mu$ m). B. *Globodera rostochiensis* (Wollenweber) cyst. C. *Heterodera* sp., two males by the needle hole (longest line = 100  $\mu$ m). D. *Heterodera hordecalis* Andersson, vulval cone top showing underbridge. E. *H. hordecalis*, vulval cone showing vulval slit separating fenestrae. F. *Heterodera bifenestra* Cooper, vulval cone top showing bullae. G. *H. bifenestra*, vulval cone top. H. *H. avenae*, en face view of second-stage juvenile. (A–C. After Siddiqi (1986). D and E. Courtesy S. Andersson. F and G. Courtesy S. Andersson and W.M. Wouts. H. Courtesy A.R. Stone).

- H. bifenestra* Cooper, 1955  
 syn. *Bidera bifenestra* (Cooper) Krall & Krall, 1978  
*Heterodera longicaudata* Seidel, 1972  
*Bidera longicaudata* (Seidel) Krall & Krall, 1978
- H. cajani* Koshy, 1967  
 syn. *Heterodera vigni* Edward & Misra, 1968
- H. canadensis* Mulvey, 1979
- H. cardiolata* Kirjanova & Ivanova, 1969
- H. carotae* Jones, 1950
- H. ciceri* Vovlas, Greco & Di Vito, 1985
- H. cruciferae* Franklin, 1945
- H. cynodontis* Shahina & Maqbool, 1989
- H. cyperi* Golden, Rau & Cobb, 1962
- H. daverti* Wouts & Sturhan, 1979
- H. delvii* Jairajpuri, Khan, Setty & Govindu, 1979
- H. elachista* Ohshima, 1974
- H. fici* Kirjanova, 1954  
 syn. *Heterodera humuli fici* Kirjanova (Merny, 1965)
- H. filipjevi* (Madzhidov, 1981) Stelter, 1984k  
 syn. *Bidera filipjevi* Madzhidov, 1981  
*Heterodera filipjevi* (Madzhidov) Stone, 1985  
*Heterodera filipjevi* (Madzhidov) Siddiqi, 1986
- H. gambiensis* Merny & Netscher, 1976
- H. glycines* Ichinohe, 1952
- H. glycyrrhizae* Narbaev, 1987
- H. goettingiana* Liebscher, 1892
- H. graminis* Stynes, 1971
- H. graminophila* Golden & Birchfield, 1972
- H. hordecalis* Andersson, 1975  
 syn. *Bidera hordecalis* (Andersson) Krall & Krall, 1978
- H. humuli* Filipjev, 1934  
 syn. *Heterodera humuli humuli* Filipjev (Merny, 1965)
- H. iri* Mathews, 1971  
 syn. *Bidera iri* (Mathews) Krall & Krall, 1978
- H. kirjanovae* Narbaev, 1988
- H. latipons* Franklin, 1969  
 syn. *Bidera latipons* (Franklin) Krall & Krall, 1978  
*Ephippiodera latipons* (Franklin) Shagalina & Krall, 1981
- H. lespedezae* Golden & Cobb, 1963
- H. leuceilyma* Di Edwardo & Perry, 1964
- H. limonii* Cooper, 1955
- H. litoralis* Wouts & Sturhan, 1996
- H. longicollum* Golden & Dickerson, 1973
- H. mani* Mathews, 1971  
 syn. *Bidera mani* (Mathews) Krall & Krall, 1978
- H. medicaginis* Kirjanova in Kirjanova & Krall, 1971
- H. mediterranea* Vovlas, Inserra & Stone, 1981

- H. menthae* Kirjanova & Narbaev, 1977  
*H. mothi* Khan & Husain, 1965  
*H. oryzae* Luc & Berdon Brizuela, 1961  
*H. oryzicola* Rao & Jayaprakash, 1978  
*H. oxiana* Kirjanova, 1962  
*H. pakistanensis* Maqbool & Shahina, 1986  
*H. phragmitidis* Kazachenko, 1986  
*H. plantaginis* Narbaev & Sidikov, 1987  
*H. raskii* Basnet & Jayaprakash, 1984  
*H. riparia* Subbotin, Sturhan, Waeyenberge & Moens, 1997  
*H. rosii* Duggan & Brennan, 1966  
*H. sacchari* Luc & Merny, 1963  
*H. salixophila* Kirjanova, 1969  
*H. sinensis* Chen PinSang, Zheng JingWu & DeLiang, 1994  
*H. skohensis* Kaushal, Sharma & Singh, 2000  
*H. sonchophila* Kirjanova, Krall & Krall, 1976  
*H. sorghi* Jain, Sethi, Swarup & Srivastava, 1982  
*H. spinicauda* Wouts, Schoemaker, Sturhan & Burrows, 1995  
*H. swarupi* Sharma, Siddiqi, Rahaman, Ali & Ansari, 1999  
*H. tadshikistanica* Kirjanova & Ivanova, 1966  
*H. trifolii* Goffart, 1932  
     syn. *Heterodera schachtii* var. *trifolii* Goffart, 1932  
         *Heterodera schachtii* galeopsidis Goffart, 1936  
         *Heterodera galeopsidis* Goffart, 1936  
         *Heterodera paratrifolii* Kirjanova, 1963  
         *Heterodera ruminis* Poghossian, 1961  
         *Heterodera scleranthii* Kaktina, 1957  
*H. turangae* Narbaev, 1988  
*H. turcomanica* Kirjanova & Shagalina, 1965  
     syn. *Bidera turcomanica* (Kirjanova & Shagalina) Krall & Krall, 1978  
         *Ephippiodera turcomanica* (Kirjanova & Shagalina) Shagalina & Krall, 1981  
*H. urticae* Cooper, 1955  
*H. uzbekistanica* Narbaev, 1980  
*H. zaeae* Koshy, Swarup & Sethi, 1971

#### Species inquirendae

- H. graduni* Kirjanova in Kirjanova & Krall, 1971  
*H. methwoldensis* Cooper, 1955  
*H. polygoni* Cooper, 1955

#### Nomina nuda

- Heterodera indocyperi* Husain & Khan, 1964  
*H. mexicana* Campos Vela, 1968  
*H. schachtii* var. *avenae* Mortensen, Rostrup & Kølpin Ravn, 1908

#### Remarks

*Heterodera* spp. are probably as important in attacking and damaging field crops in



cold temperate regions as are *Meloidogyne* spp. in the tropics. However, about 24 species of *Heterodera* are now known from the tropics. Their popular names, in most instances, suggest their host preference. For example, *H. avenae*, *H. glycines*, *H. goettingiana*, *H. schachtii* and *H. trifolii* are called, cereal, soybean, pea, sugarbeet and clover cyst nematodes, respectively. Several species (e.g. *H. galeopsidis*, *H. glycines*, *H. schachtii*, *H. trifolii*) are parasites of Caryophyllaceae, Leguminosae and Polygonaceae. Several species parasitize Gramineae: *H. avenae* attacks a number of grasses in Europe where it appears to be indigenous. *Heterodera cyperi*, *H. graminophila*, *H. graminis*, *H. hordecalis*, *H. iri*, *H. latipons*, *H. mani*, *H. moths* and *H. raskii* are grass parasites. Those that attack monocot field crops are *H. oryzae* and *H. oryzicola* on rice; *H. sacchari* on sugarcane; *H. delvii*, *H. gambiensis* and *H. sorghi* on millets and *H. zae* on maize. *Heterodera zae* is a major pest of maize in India, Pakistan and Egypt and is also found in the USA where maize is cultivated in large areas. *Heterodera glycines* is a major pathogen of soybeans in Japan, northeastern China and the USA, as is *H. cajani* on pulse crops in India.

*Heterodera mediterranea*, which parasitizes woody host species (olive and pistachio) in Italy, differs from most other cyst nematodes in being ectoparasitic, with juveniles and adults never found completely embedded in root tissues. Ectoparasitism of roots is also known to occur in *H. sacchari* and occasionally in *H. avenae* and *H. schachtii*, and is an ancestral trait of the Heteroderidae.

Species previously attributed to *Ehippiodera* are mostly European in distribution. *Ehippiodera turkomanica* was described on some cysts found in soil (host plant not known) from Ashqabad, Turkmenia. It has been found on Turkmenian desert trees and shrubs; the two most common host plants are *Salsola richteri* Karel. and *S. pazetzkiana* Litv. of the Chenopodiaceae. Occasionally members of Polygonaceae and Zygophyllaceae are also attacked, but not the grasses. *Ehippiodera latipons*, on the other hand, parasitizes grasses, wheat, oat and rye in Italy, Libya, Bulgaria, Israel, Spain, Poland and Great Britain. *Ehippiodera* spp. (especially *E. latipons*) are morphologically close to *Heterodera avenae*, the type species of the genus *Bidera* Krall & Krall, 1978 and both *Ehippiodera* and *Bidera* are considered here as junior synonyms of *Heterodera*.

The type species was found on sugarbeet (*Beta vulgaris* L.) at Aschersleben, Germany and is well distributed on this host in Europe. Keys to species of *Heterodera*, *Bidera* and *Meloidodera*, and *Heterodera*, *Globodera*, *Cactodera* and *Punctodera* were given by Wouts *et al.* (1986) and Golden (1986), respectively.

ETYMOLOGY. From Greek *heteros* = other, and *deras* = skin, as modified by Schmidt (1871) to the Latin, feminine gender (refers to the different 'skins' of female and cyst).

## Genus *Cactodera* Krall & Krall, 1978

(Fig. 87, M–P)

### Diagnosis

Heteroderinae. **Mature female and cyst:** Spherical, with small **terminal protuberance** (vulval cone) in mature female; females yellowish, cysts dark brown. Cuticular surface pattern characteristic, with **roughly parallel ridges** interrupted by short vertical or oblique ridges; **D-layer present** (absent in *C. betulae*). Vulval slit short

(13–20  $\mu\text{m}$ ). Vulval fenestra **circumfenestrate**, 20–48  $\mu\text{m}$  in diameter; bullae and underbridge absent; **vulval denticles usually present**. No anal fenestration. **Eggs with punctate surface** (type species) or without visible marking; all eggs (about 300–400) retained in the cyst; no egg mass formed. **Male:** Length up to 1.7 mm; posterior end twisted. Labial disc present but not prominent. Stylet 26–29  $\mu\text{m}$ ; spicules 32–36  $\mu\text{m}$  long, distally pointed with bifid tip; gubernaculum 10–12  $\mu\text{m}$  long in the type species. Tail less than one-half body width long, rounded; cloacal lips not forming a tube. **Second-stage juvenile:** Body 0.42–0.63 mm, stylet 22–28  $\mu\text{m}$  and tail 34–38  $\mu\text{m}$  long in type species. Lateral field with four incisures. Labial disc present but not conspicuous; generally six lip sectors present. Oesophageal glands filling body cavity. Tail conical, terminal half hyaline. Phasmid punctiform, without a lens-like structure in muscle layer. **Feeding induces a syncytium, generally with wall ingrowths.**

### Type species

*Cactodera cacti* (Filipjev & Schuurmans Stekhoven, 1941) Krall & Krall, 1978  
syn. *Heterodera cacti* Filipjev & Schuurmans Stekhoven, 1941

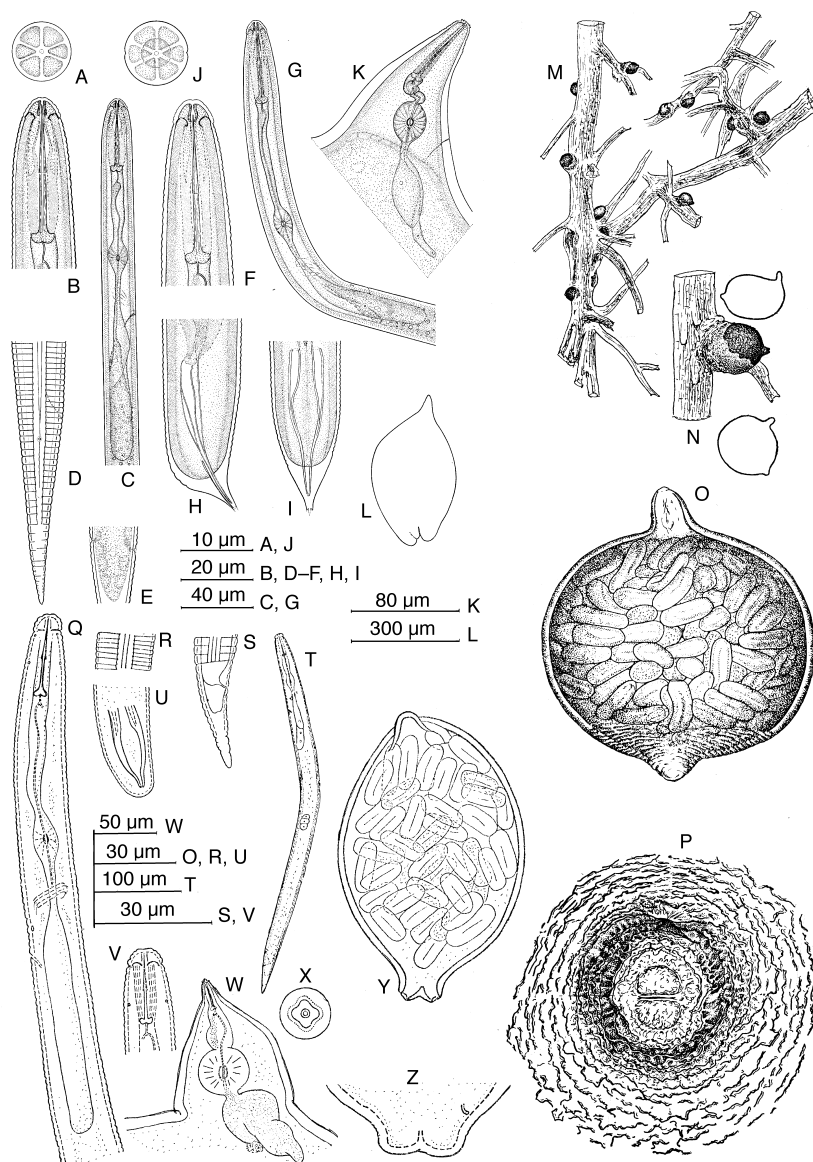
### Other species

*Cactodera acnidae* (Schuster & Brezina, 1979) Wouts, 1985  
syn. *Heterodera acnidae* Schuster & Brezina, 1979  
*C. amaranthi* (Stoyanov, 1972) Krall & Krall, 1978  
syn. *Heterodera amaranthi* Stoyanov, 1972  
*C. aquatica* (Kirjanova, 1971) Krall & Krall, 1978  
syn. *Heterodera aquatica* Kirjanova, 1971  
*C. betulae* (Hirschmann & Riggs, 1969) Krall & Krall, 1978  
syn. *Heterodera betulae* Hirschmann & Riggs, 1969  
*C. eremica* Baldwin & Bell, 1985  
*C. estonica* (Kirjanova & Krall, 1963) Krall & Krall, 1978  
syn. *Heterodera estonica* Kirjanova & Krall, 1963  
*C. milleri* Graney & Bird, 1990  
*C. salina* Baldwin, Mundo-Ocampo & McClure, 1997  
*C. thornei* (Golden & Raski, 1977) Krall & Krall, 1978  
syn. *Heterodera thornei* Golden & Raski, 1977  
*C. weissii* (Steiner, 1949) Krall & Krall, 1978  
syn. *Heterodera weissii* Steiner, 1949

### Note

The genus is supposed to have originated in Mexico and is distributed mainly in Central America, southern parts of North America and in the arid zones of north and central regions of South America (Krall & Krall, 1978). *Cactodera cacti* and *C. estonica* occur in many European countries in glasshouses on ornamental plants. The life cycle of *C. cacti* is completed in 29–34 days at 18–26°C. A key to species is given by Graney and Bird (1990).

ETYMOLOGY. From specific epithet of type species name *cacti*, and Greek *deras* = skin, modified to the Latin feminine, as for *Heterodera*.



**Fig. 87.** A–L. *Sarisodera hydrophila* Wouts & Sher. M–P. *Cactodera cacti* (Filipjev & Schuurmans Stekhoven). Q–Z. *Heterodera* (=Ephippiodera) *turcomanica* (Kirjanova & Shagalina). A. *En face* view of juvenile. B and V. Head ends of juveniles. C. Oesophagus of second-stage juvenile. D and S. Tail ends of second-stage juveniles. E. Phasmids of juvenile, ventral view. F. Head end of male. G and Q. Oesophageal regions of males. H, I and U. Tail ends of males. J and X. *En face* views of females. K and W. Oesophageal regions of females. L. Female. M. Females on roots of *Phyllocactus* sp. N, O and Y. Cysts. P and Z. Vulval cone tops. R. Lateral field of male. T. Second-stage juvenile. (A–L. After Wouts & Sher (1971), courtesy *Journal of Nematology*. M–P. After Kirjanova & Terenteva (1961). Q–Z. After Shagalina & Krall (1981).)

The type species was found on cactus plants (*Phyllocactus akkermanni* and *Cereus speciosus*) in Holland and reported as *Heterodera schachtii*. It is known from a number of countries and may be cosmopolitan. *Cactodera weissi* was found on knot-weed (*Polygonum pennsylvanicum* L.) in Maryland, USA, and occurs in several places in the USA and Canada. *Cactodera armaranthi* and *C. thornei*, also from the USA, were found on *Amaranthus viridis* L. and *Montia perfoliata* (miner's lettuce). *Cactodera salina* was found parasitizing *Salicornia bigelovii* in Mexico. *Cactodera estonica* (type host not known) occurs on grasses in Estonia, Poland, Turkey and Yugoslavia.

### Genus *Afenestrata* Baldwin & Bell, 1985

syn. *Afrodera* Wouts, 1985

*Brevicephalodera* Kaushal & Swarup, 1989; syn. n.

(Fig. 88)

#### Diagnosis

Heteroderinae. **Female** spherical, subspherical or when mature lemon-shaped, with a short projecting neck. Cuticle relatively thin, striated or bearing lace-like pattern on surface; **D-layer absent**. **Vulva terminal, on a cone-like protuberance, with prominent lips; vulval slit may be deeply sunken**. **Cyst stage present; cyst without vulval fenestra and bullae**; underbridge present or absent. No anal fenestration. Male body twisted in posterior region, with four incisures in lateral field, stylet 24–28 µm long, straight spicules directed posteriorly and a **cloacal tubus**; **tail absent**; phasmids not seen. Juveniles with three or four incisures, stylet less than 30 µm long, oesophageal glands filling body cavity width and **pore-like phasmids devoid of a lens-like structure**. **Feeding induces formation of syncytium with walls lacking ingrowths**.

#### Type species

*Afenestrata africana* (Luc, Germani & Netscher, 1973) Baldwin & Bell, 1985

syn. *Sarisodera africana* Luc, Germani & Netscher, 1973

*Afrodera africana* (Luc et al.) Wouts, 1985

#### Other species

*Afenestrata axonopi* Souza, 1996

*A. bamboosi* (Kaushal & Swarup, 1989) comb. n.

syn. *Brevicephalodera bamboosi* Kaushal & Swarup, 1989

*Heterodera bamboosi* (Kaushal & Swarup) Wouts & Baldwin, 1998

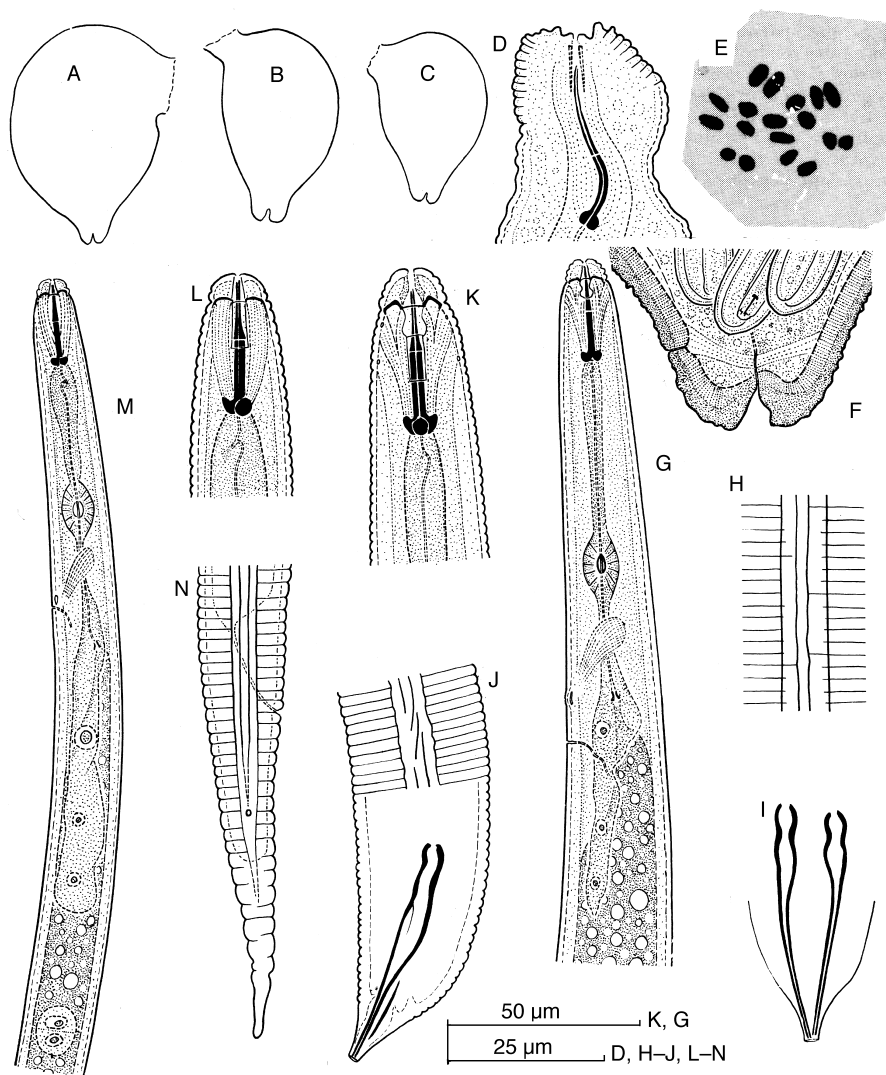
*A. koreana* Vovlas, Lamberti & Choo, 1992

*A. orientalis* Kazachenko, 1989

*A. sacchari* Kaushal & Swarup, 1989

#### Remarks

*Afrodera* is an objective junior synonym of *Afenestrata*, being based on the same type species. Siddiqi (1986) synonymized *Afenestrata* to *Sarisodera* but Luc et al. (1988) upheld its validity on the grounds of *Afenestrata africana* having a cyst stage, inciting a syncytium, lacking a D-layer in the female cuticle and punctiform phasmids devoid of a lens-like structure in juveniles.



**Fig. 88.** *Afenestrata africana* (Luc, Germani & Netscher). A–C. Mature females. D. Head end of mature female. E. Pairing of chromosomes in telephase. F. Terminal (cone) region of female. G and M. Oesophageal regions of male and second-stage juvenile, respectively. H. Lateral field of male. I and J. Terminal region showing spicules and penial tube. K and L. Head end of male and second-stage juvenile, respectively. N. Tail end of second-stage juvenile. (After Luc *et al.* (1973), courtesy Cahiers ORSTOM.)

Souza (1996) discussed the relationship between *Afenestrata* and *Brevicephalodera* Kaushal & Swarup, 1989 stating that the distinction between the two was doubtful. *Brevicephalodera bamboosi* described from bamboo (*Bamboosa* sp.) in Assam State, India has a female with an elongate-oval body, which is kidney-shaped due to a depressed ventral side; the vulval area is depressed, with no terminal cone formation;

the vulva is terminal, sunken, with hypertrophied lips and no fenestration. Wouts & Baldwin (1998) placed *B. bamboosi* in *Heterodera* as a new combination because in the original description some fenestration around the vulval slit was reported. The species is here transferred to *Afenestrata* and *Brevicephalodera* is synonymized with it.

In the roots of bamboo (*Phyllostachys pubescens*) in Korea, *Afenestrata koreana* induces the formation of a stelar syncytium of several interconnected cells which are two to three times larger than normal adjacent cells. Syncytia cell walls lack ingrowths, resembling those induced by certain species of *Rotylenchulus* (e.g. *R. reniformis* and *R. borealis*).

ETYMOLOGY. A = without, and *fenestrata* = bearing fenestra, refers to the absence of vulval fenestration.

The type species was described from *Panicum maximum* (imported from Kenya) growing in an experimental field at ORSTOM Centre at Adiopodoumé, Côte d'Ivoire. *Afenestrata axonopi* parasitizes the grass, *Axonopus marginatus*, in Brazil. *Afenestrata orientalis* was found parasitizing roots of *Miscanthus purpureus* near a lake in Kazan district, Far Eastern Russia.

### Genus *Globodera* Skarbilovich, 1959 (Behrens, 1975)

syn. *Heterodera* (*Globodera* Skarbilovich, 1959)

(Figs 86, B; 89)

#### Diagnosis

Heteroderinae. **Mature female and cyst:** Spheroidal with a short projecting neck, **terminal region not forming a cone**. Cyst brown, **surface with a lace-like pattern**. Cuticle thick, with D-layer. Vulva terminal; slit length less than 15 µm long, usually lost from old cysts; **tuberculate area near vulva present**. Vulval fenestra **circum-fenestrate**. Vaginal remnant **underbridge and bullae absent, rudiments rarely present**. Anus dorsally subterminal, not on dorsal lip, separated from vulva by a short distance, but both lie in a terminal 'vulval basin'. No anal fenestra. Eggs retained in body; **no egg mass formed**. **Male:** Up to 1.5 mm long; posterior end spirally twisted through 90–180°. Cuticle annulated; lateral field with four incisures, outer bands often areolated. Cephalic region offset by constriction, with indistinct labial disc, and three to seven annules. Spicules over 30 µm long, **with single pointed tip**. Tail short, hemispherical; cloacal lips not forming a tube. **Second-stage juvenile:** As for *Heterodera*, but, in SEM, labial disc subcircular; distinct lip sectors present. Stylet less than 30 µm long. Oesophageal glands fill the body cavity. Tail conically pointed, with hyaline portion about half its total length. Phasmid punctiform, without a lens-like structure. **Feeding induces a syncytium.**

#### Type species

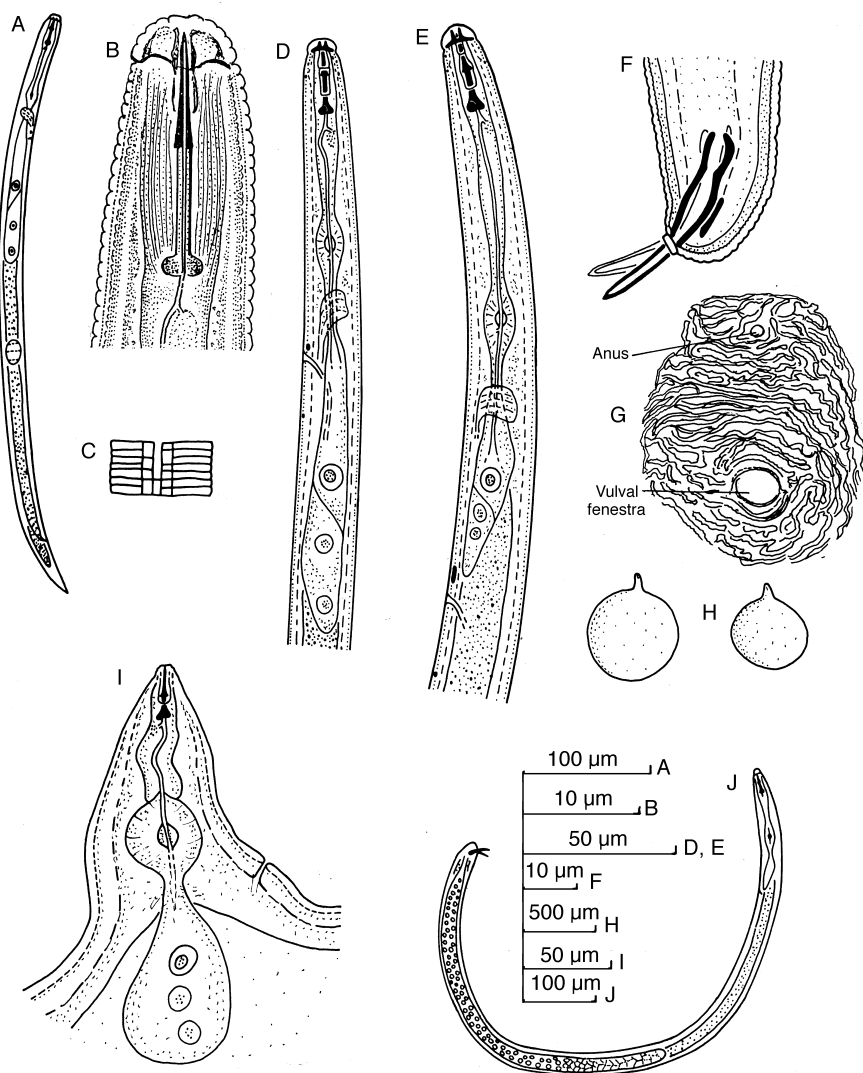
*Globodera rostochiensis* (Wollenweber, 1923) Skarbilovich, 1959

syn. *Heterodera schachtii rostochiensis* Wollenweber, 1923

*Globodera rostochiensis* (Wollenweber) Behrens, 1975

*Globodera rostochiensis* (Wollenweber) Mulvey & Stone, 1976

*Heterodera schachtii solani* Zimmermann, 1927



**Fig. 89.** *Globodera rostochiensis* (Wollenweber). A. Second-stage juvenile. B. Head end of second-stage juvenile. C. Lateral field of juvenile. D and E. Oesophageal regions of second-stage juvenile and male, respectively. F. Tail end of male. G. Perineal region of cyst showing vulval fenestra, anus and cuticular ridges. H. Cysts. I. Oesophageal region of female. J. Male. (B and G. Original, remainder after Stone, 1973.)

### Other species

*Globodera achilleae* (Golden & Klindić 1973) Behrens, 1975

syn. *Heterodera achilleae* Golden & Klindić 1973

*Globodera achilleae* (Golden & Klindić) Mulvey & Stone, 1976

*G. artemisiae* (Eroshenko & Kazachenko, 1972) Behrens, 1975

- syn. *Heterodera artemisiae* Eroshenko & Kazachenko, 1972  
*Globodera artemisiae* (Eroshenko & Kazachenko) Mulvey & Stone, 1976
- G. *chuabattia* (Gupta & Edward, 1973) Wouts, 1984  
 syn. *Heterodera chaubattia* Gupta & Edward, 1973  
*Heterodera mali* Kirjanova & Borisenko, 1975  
*Globodera mali* (Kirjanova & Borisenko) Behrens, 1975  
*Globodera mali* (Kirjanova & Borisenko) Mulvey & Stone, 1976
- G. *hypolysi* Ogawa, Ohshima & Ichinohe, 1983
- G. *leptonepia* (Cobb & Taylor, 1953) Skarbilovich, 1959  
 syn. *Heterodera leptonepia* Cobb & Taylor, 1953  
*Globodera leptonepia* (Cobb & Taylor) Behrens, 1975  
*Globodera leptonepia* (Cobb & Taylor) Mulvey & Stone, 1976
- G. *millefolii* (Kirjanova & Krall, 1965) Behrens, 1975 (= sp. inq. for Krall, 1978)  
 syn. *Heterodera millefolii* Kirjanova & Krall, 1965  
*Globodera millefolii* (Kirjanova & Krall) Mulvey & Stone, 1976
- G. *mirabilis* (Kirjanova, 1971) Mulvey & Stone, 1976  
 syn. *Heterodera mirabilis* Kirjanova, 1971
- G. *pallida* (Stone, 1973) Behrens, 1975  
 syn. *Heterodera pallida* Stone, 1973 (based on B and E pathotypes of English designation of *Heterodera rostochiensis*)  
*Globodera pallida* (Stone) Mulvey & Stone, 1976
- G. *pseudorostochiensis* (Kirjanova, 1963) Mulvey & Stone, 1976 (a probable syn. of *H. rostochiensis* for Krall, 1978)  
 syn. *Heterodera pseudorostochiensis* Kirjanova, 1963
- G. *tabacum solanacearum* (Miller & Gray, 1972) Behrens, 1975  
 syn. *Heterodera solanacearum* Miller & Gray, 1972  
*Heterodera tabacum solanacearum* Miller & Gray (Stone, 1983)  
*Globodera solanacearum* (Miller & Gray) Behrens, 1975  
*Globodera solanacearum* (Miller & Gray) Mulvey & Stone, 1976
- G. *tabacum tabacum* (Lownsbery & Lownsbery, 1954) Skarbilovich, 1959  
 syn. *Heterodera tabacum* Lownsbery & Lownsbery, 1954  
*Globodera tabacum* (Lownsbery & Lownsbery) Skarbilovich, 1959  
*Globodera tabacum* (Lownsbery & Lownsbery) Behrens, 1975  
*Globodera tabacum* (Lownsbery & Lownsbery) Mulvey & Stone, 1976
- G. *tabacum virginiae* (Miller & Gray, 1968) Stone, 1973  
 syn. *Heterodera virginiae* Miller & Gray, 1968  
*Heterodera tabacum virginiae* Miller & Gray (Stone, 1983)  
*Globodera virginiae* (Miller & Gray) Stone, 1973  
*Globodera virginiae* (Miller & Gray) Behrens, 1975  
*Globodera virginiae* (Miller & Gray) Mulvey & Stone, 1976
- G. *zelandica* Wouts, 1984

## Notes

On the basis of the cyst shape, Skarbilovich (1959) proposed the subgenera *Heterodera* and *Globodera* of the genus *Heterodera*. Behrens raised the *Globodera* to genus and proposed new combinations with *Globodera* for the species listed by Skarbilovich under *Heterodera* (*Globodera*). Later Mulvey & Stone (1976) also pro-



posed to raise the subgenus *Globodera* to genus. Yadav & Verma (1983) also proposed new combinations of the above species with *Globodera* but these have not been listed above.

Loof & Bakker (1992) pointed out that Stone (1973), who described *Heterodera pallida*, had stated in the abstract of the paper that it belonged to the subgenus *Globodera*; on p. 603 he had stated: 'The *Heterodera* (*Globodera*) species with solanaceous hosts (*H. pallida*, ... *H. tabacum*, ... *H. virginiae* ...)'. Loof & Bakker stated: 'The Secretariat of the International Commission on Zoological Nomenclature, on being consulted on this point, stated that the above phrases are sufficient to consider Stone (1973) as author of the combinations *Globodera pallida* (*in litt.*, January 20, 1989) and *G. virginiae* (*in litt.*, February 19, 1990).' Similarly, Skarbilovich (1959), who erected the subgenus *Globodera* with *Heterodera rostochiensis* as its type species, has, in effect, erected the genus *Globodera* with *G. rostochiensis* as its type species. Skarbilovich also combined the species name *leptonepia*, *tabacum* and *punctata* (now in *Punctodera*) with the subgenus name *Globodera* and so, Loof & Bakker stated: '... it is legitimate deduction (confirmed in correspondence with the Secretariat of the International Commission on Zoological Nomenclature) that she [Skarbilovich] combined these specific names not only with the subgeneric name *Globodera* but also with the generic name *Globodera*. Thus the combinations *G. rostochiensis*, *G. leptonepia* and *G. tabacum* are to be attributed to her.'

Research work in the past 45 years has provided much information on the distribution, biology, host-parasite relationships and control of the potato cyst nematodes and the menace is well under control in Western Europe and the USA, mainly due to stringent phytosanitary regulations for potato cultivation and transportation. *Globodera solanacearum*, *G. tabacum* and *G. virginiae*, described from the USA, are similar to the potato cyst nematodes in morphology and host preference and their differentiation is often difficult. They are considered here as subspecies of *G. tabacum* which attacks tobacco, tomato and several other hosts. *Globodera millefolii* and *G. mirabilis* may be junior synonyms of *G. achilleae*. Like *G. rostochiensis*, the *G. tabacum* complex prefers members of the family Solanaceae; it occurs mostly in the USA and China. Wouts (1984) and Golden (1986) gave keys to species of *Globodera*.

ETYMOLOGY. From Latin *globus* = globe, and Greek *deras* = skin, modified into Latin feminine, as for *Heterodera*.

The type species was found on *Solanum tuberosum* L. in Rostock, Germany. *Globodera* spp. parasitize Solanaceae and Compositae and are almost cosmopolitan. The potato cyst nematodes (*G. rostochiensis* and *G. pallida*) are a menace to potato growers in Europe and other parts of the world. *Globodera pallida* seems to be more adapted to lower temperatures than *G. rostochiensis* as its larvae hatch in lower temperatures (15–20°C vs. 20–25°C). Both are supposed to have originated in the Andean region of Peru, where they are indigenous on wild Solanaceae, and to have

been introduced with the potatoes into Europe and from there into the east coast of the USA, India and the Far East.

**Genus *Punctodera* Mulvey & Stone, 1976**  
**(*Punctodera* Krall & Krall, 1973 = *nomen nudum*)**  
(Fig. 90, E & F)

**Diagnosis**

Heteroderinae. **Mature female and cyst:** Spherical, pear-shaped or oval, with a short projecting neck, and heavy subcrystalline layer. Cuticle reticulate, **subcuticle with punctations. D-layer present. Terminal region not cone-shaped;** cyst light to dark brown. **Vulval slit extremely short** (less than 5  $\mu\text{m}$ ); anus at a short distance from vulval lip. Circumfenestrate, fenestra surrounding vulva 16–40  $\mu\text{m}$  (about 20  $\mu\text{m}$  in type species) in diameter; anus offset towards ventral margin of fenestra; **an anal fenestra of similar shape and size as vulval fenestra present.** Underbridge and perineal papillae-like tubercles absent. Bullae usually absent. Eggs retained in body, no egg sac is formed. **Male:** Vermiform, under 1.5 mm long. Labial disc present but not prominent. Stylet well developed, 23–28  $\mu\text{m}$  long. Orifice of dorsal oesophageal gland 2.6–4.6  $\mu\text{m}$  behind stylet base. Spicules 31–33  $\mu\text{m}$  long, distally pointed. Tail less than half anal body width long; cloacal lips not forming a tube. **Second-stage juvenile:** Body 0.35–0.49 mm, stylet 24–26  $\mu\text{m}$  and tail conical, 63–78  $\mu\text{m}$  long with a 38–41  $\mu\text{m}$  long hyaline terminal portion in type species. Lateral field with three or four incisures. Oesophageal glands fill body width. Phasmids punctiform, without a lens-like structure. **Feeding induces a syncytium.**

**Type species**

*Punctodera punctata* (Thorne, 1928) Mulvey & Stone, 1976  
syn. *Heterodera punctata* Thorne, 1928  
*Globodera punctata* (Thorne, 1928) Skarbilovich, 1959

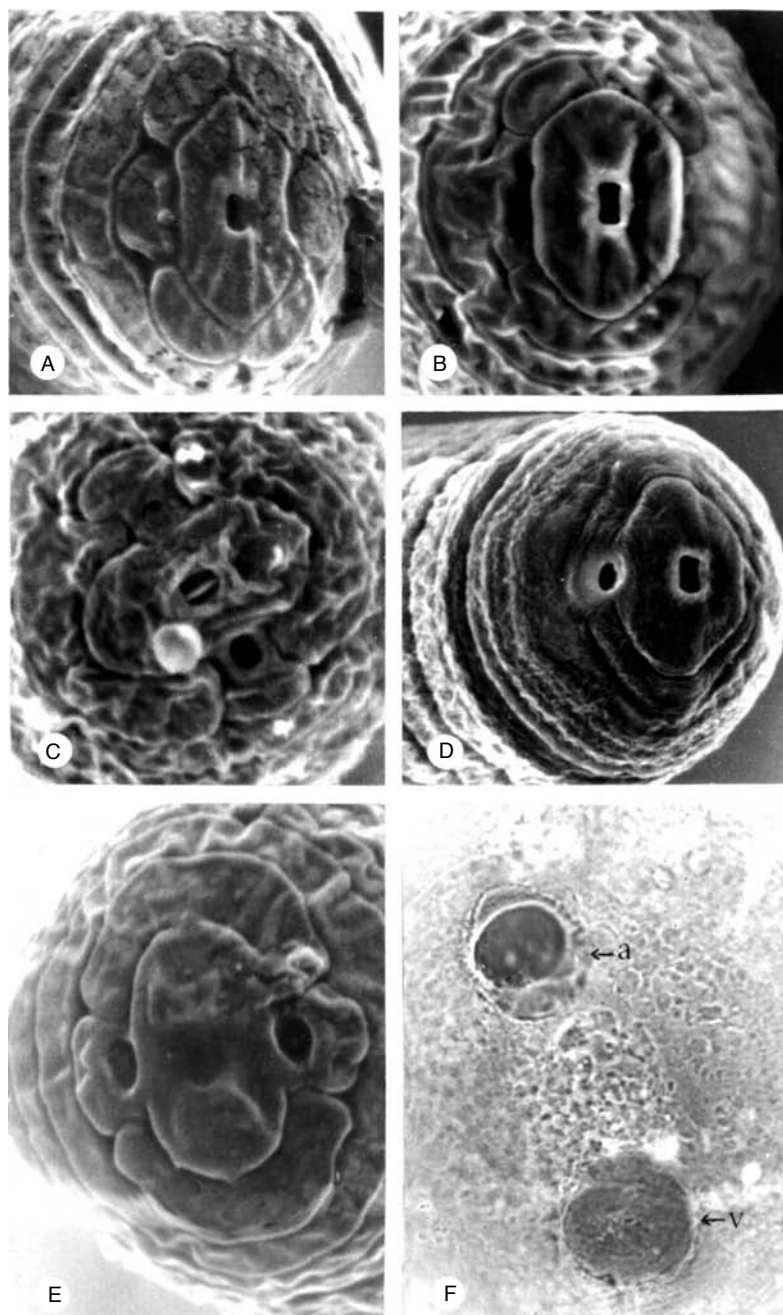
**Other species**

*Punctodera chaltoensis* Stone, Sosa Moss & Mulvey, 1976  
*P. matadorensis* Mulvey & Stone, 1976

**Note**

A multivariate analysis of variance of seven most significant morphological characters of second-stage juveniles of *Punctodera punctata* in several populations from Europe showed that two morphologically distinct groups, which may represent two different species, are present (Wouts *et al.*, 1986). Brzeski (1998) suggested revision of the genus as several different species were probably covered by the type species name.

ETYMOLOGY. From specific epithet of type species, referring to punctations of the subcuticle, and Greek *deras* = skin, feminine gender as for *Heterodera*.



**Fig. 90.** A–E. Scanning electron micrographs of head *en face* of second-stage juveniles. A. *Meloidodera charis* Hopper. B. *Cryphodera eucalypti* Colbran. C. *Atalodera ucui* Wouts & Sher. D. *Sarisodera hydrophila* Wouts & Sher. E. *Punctodera chalcoensis* Stone, Sosa Moss & Mulvey. F. *Punctodera chalcoensis*, perineal region showing anal (a) and vulval (V) fenestrae. (A–D. After Stone (1975). E. After Stone *et al.* (1976), courtesy *Nematologica*.)

*Punctodera* spp. parasitize Gramineae (barley, grasses, oats, wheat). The type species was found on wheat and grass roots in Saskatchewan, Canada, and is commonly found on grasses in Canada and Europe. *Punctodera punctata* is a pest of wheat in UK and Canada and *P. chaltoensis* is an important parasite of maize in Mexico, sometimes causing almost 100% loss in maize yield. *Punctodera matadorensis* is a little-known species that parasitizes grasses in Saskatchewan, Canada. The genus is believed to be of ancient origin, in North America (Krall & Krall, 1978).

### Genus *Dolichodera* Mulvey & Ebsary, 1980

(Fig. 91, C, M–R)

#### Diagnosis

Heteroderinae. **Female:** Body elongate-oval, without terminal protuberance, white, swollen part 400–500  $\mu\text{m}$  long, 140–270  $\mu\text{m}$  wide; 2–2.8 times as long as wide; neck moderately long. Cuticle 3–4  $\mu\text{m}$  thick, not annulated but with fine irregular striae. Vulval area terminal or just subterminal, circumfenestrate, fenestra about 20  $\mu\text{m}$  in diameter; **bullae present, perineal tubercles absent**. Anus pore-like, lacking a fenestra, 10–13  $\mu\text{m}$  dorsal to vulval fenestral margin. Stylet well developed, 15  $\mu\text{m}$  long in type species. Mature female with more than 100 eggs in various developmental stages. **Cyst:** Light brown, elongate-oval, 450–700  $\mu\text{m}$  by 140–300  $\mu\text{m}$ ; 1.8–4.0 (2.6) times as long as wide; with a long neck. Cuticle 3–4  $\mu\text{m}$  thick. **Several large-sized bullae present**. Perineal tubercles absent. Vulva circumfenestrate; underbridge absent. **Anus lacking fenestra**. Male not found. **Second-stage juvenile:** 0.57–0.61 mm long; slender ( $a = 27\text{--}31$ ), with 95–120  $\mu\text{m}$  long tail, hyaline terminal portion long. **Lateral field with three incisures**, inner one faint. Cephalic region hemispherical, set off, with two annules; sclerotization heavy. Stylet slender, 22–24  $\mu\text{m}$  long; knobs anteriorly concave. Median bulb oval, refractive thickenings small, 80–90  $\mu\text{m}$  from anterior end. Oesophageal glands elongate, ventral and ventrolateral to intestine. Tail tip narrowly rounded. Phasmids lacking a lens-like structure, about one body width behind anus. Host reaction to feeding not known.

#### Type species

*Dolichodera fluvialis* Mulvey & Ebsary, 1980

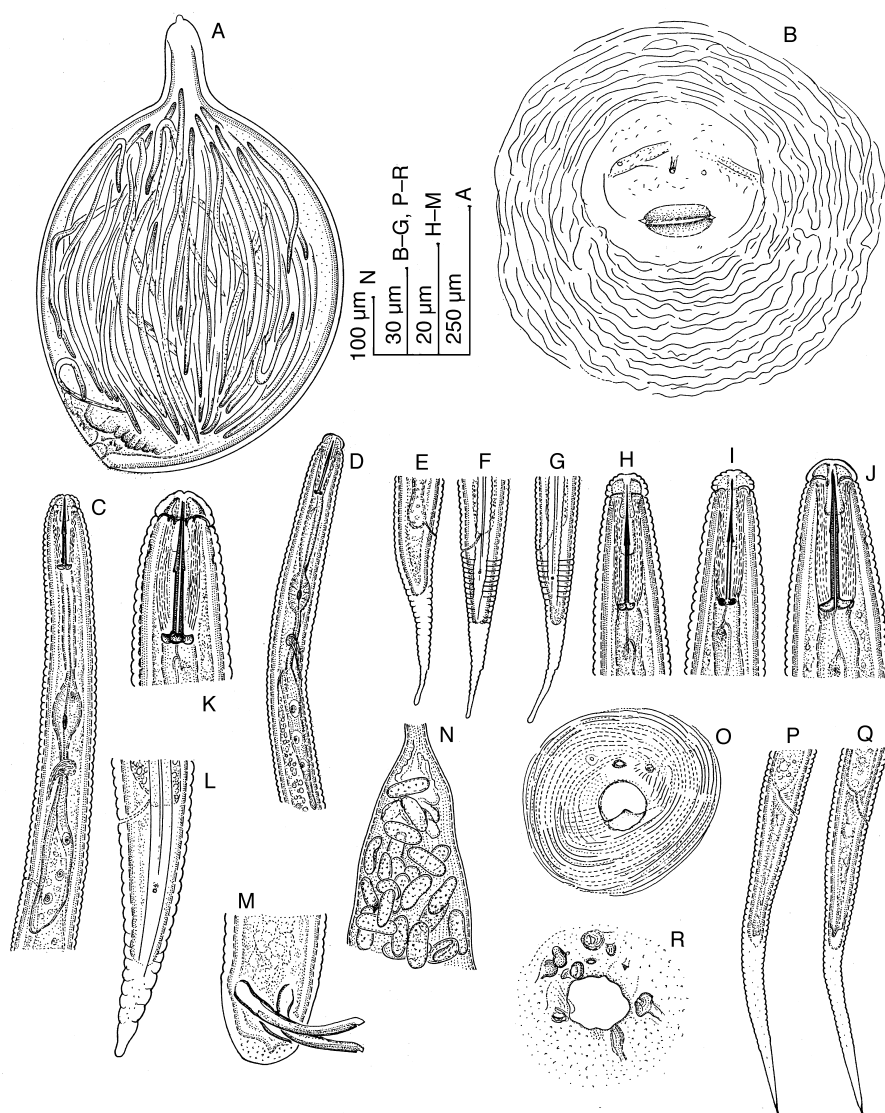
No other species.

#### Note

*Dolichodera* may be a junior synonym of *Punctodera*, the only difference being the absence of anal fenestration. Further collection and study of *D. fluvialis* is needed to solve this problem.

ETYMOLOGY. From Greek *dolichos* = long, and *deras* = skin.

The type species was found on roots of aquatic grass (*Spartina pectinata*) from the bottom of the Ottawa River near Deschenes, Canada.



**Fig. 91.** A, B, D–I. *Atalodera gracilancea* (Robbins), paratypes. J–L. *Atalodera andina* (Golden, Franco, Jatala & Astogaza). C, M–R. *Dolichodera fluvialis* Mulvey & Ebsary, paratypes. A. Mature female with juveniles. B. Vulval–anal region. C and D. Oesophageal regions of male and second-stage juvenile, respectively. E–G and L. Tail ends of second-stage juveniles. H–K. Head ends of second-stage juveniles. M. Tail end of male. N. Portion of cyst with eggs. O. Terminal region of cyst. P and Q. Tail ends of second-stage juveniles. R. Terminal region of cyst showing fenestra and bullae.

**Subfamily Meloidoderinae Golden, 1971**  
**syn. Meloidoderini Golden, 1971 (Coomans, 1979)**

**Diagnosis**

Heteroderidae. Female oval with short neck, **does not turn into a cyst**. Eggs retained in body or laid. Cuticle annulated. **Vulva almost equatorial**; anus terminal. Male small-sized, **develops without metamorphosis**. Second-stage juveniles with four incisures in lateral field. Female feeding induces uninucleate nurse cell (vs. multinucleate syncytia in other heteroderids).

**Type genus**

*Meloidodera* Chitwood, Hannon & Esser, 1956  
No other genus.

**Genus *Meloidodera* Chitwood, Hannon & Esser, 1956**

(Figs 90, A; 92, A–L)

**Diagnosis**

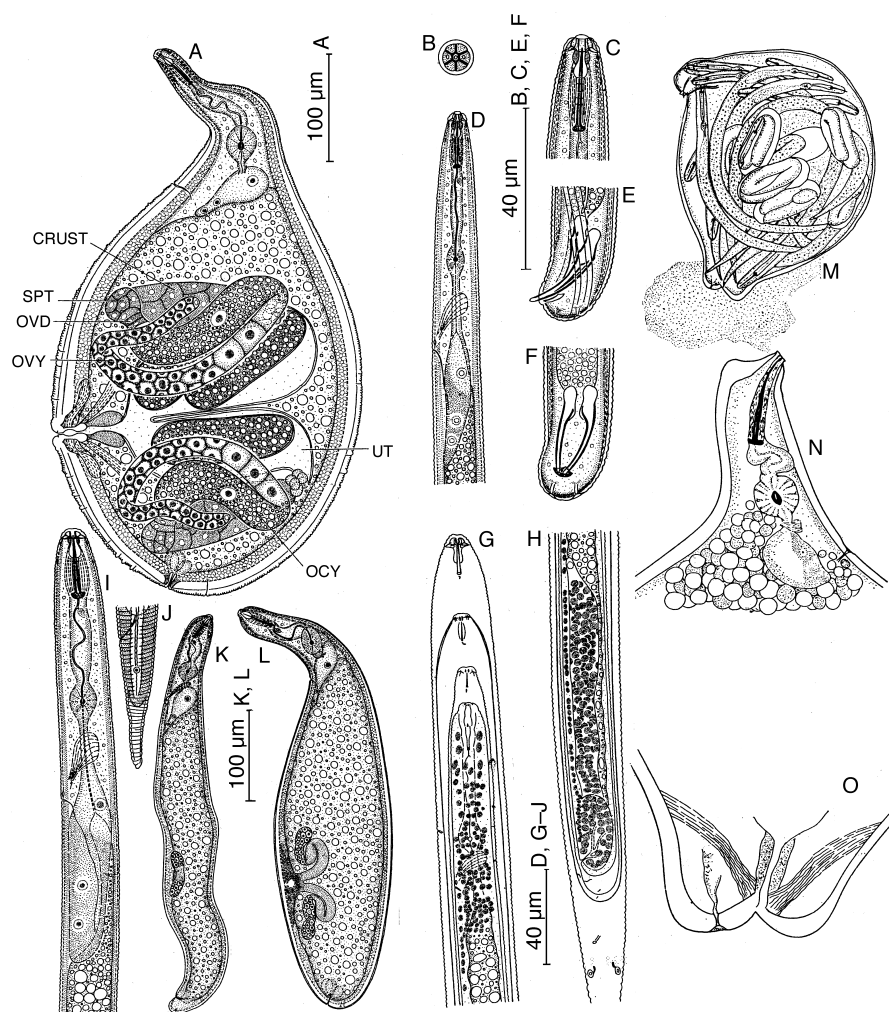
Meloidoderinae. **Mature female:** Oval, with a short neck. Cuticle annulated, except near vulva, with internal rows of punctations parallel to annules; D-layer absent. **Vulva median to submedian**. Anus ventrally subterminal or terminal; no terminal cone. **No cyst stage**; eggs laid, or some retained in body. **Male:** Under 0.6 mm long, slender. Cephalic region offset, with prominent labial disc, annulated, basal lip annule not indented (except in *M. eurytyla*); framework sclerotized, high arched, all six sectors equal in size. Stylet generally 20–25  $\mu\text{m}$  long, being shorter than that of second-stage juvenile. Median bulb fusiform. Spicules less than 30  $\mu\text{m}$  long. Tail present; anal lips not forming a tube. Bursa absent. Development of male of type species in water involved one moult in egg and three superimposed moults outside, and **no metamorphosis**. **Second-stage juvenile:** Under 0.6 mm long. Lateral field with four incisures. Cephalic region offset; labial disc indistinct. Stylet 24–35  $\mu\text{m}$  long, knobs rounded. Oesophageal glands filling body cavity width. Tail conical, hyaline part under 36  $\mu\text{m}$  long. Phasmids with a lens-like structure under muscle layer. **Feeding induces a single nurse cell.**

**Type species**

*Meloidodera floridensis* Chitwood, Hannon & Esser, 1956

**Other species**

*Meloidodera belli* Wouts, 1973  
*M. charis* Hopper, 1960  
*M. eurytyla* Bernard, 1981  
*M. hissarica* Krall & Ivanova, 1992  
*M. mexicana* Cid del Prado V., 1991  
*M. tianschanica* Ivanova & Krall, 1985  
*M. ulni* Turkina & Chizhov, 1986  
*M. zacanensis* Cid del Prado V., 1997



**Fig. 92.** A–L. *Meloidodera floridensis* Chitwood, Hannon & Esser. M–O. *Rhizonema sequoiae* Cid del Prado Vera, Lownsbery & Maggenti. A and M. Females. B. Face view at level of basal head annule of male. C. Head end of male. D. Oesophageal region of male. E and F. Tail ends of male, lateral and ventral view, respectively. G and H. Anterior and posterior regions of moulting fourth-stage male juvenile, respectively. I and J. Oesophageal region and tail of second-stage juvenile, respectively. K. Third-stage juvenile. L. Fourth-stage juvenile. N. Anterior end of female. O. Posterior cone region of female showing vulva and anus. CRUST, crustaformeria; OCY, oocyte; OVY, ovary; OVD, oviduct, SPT, spermatheca; UT, uterus. (A–L. After Hirschmann and Triantaphyllou (1973), courtesy *Journal of Nematology*. M–O. After Cid del Prado Vera *et al.* (1983).).

## Species inquirendae

*Meloidodera armeniaca* Poghossian, 1960

*M. sikhotealiniensis* Eroshenko, 1978

*M. tadzhikistanica* Kirjanova & Ivanova, 1966

ETYMOLOGY. From prefix of *Meloidogyne*, and suffix of *Heterodera*.

The type species was found on roots of slash pine, *Pinus elliottii* Englm., in Florida, USA. It has since been found on several *Pinus* species in various places in the USA. *Meloidodera charis* occurred on honey mesquite, *Prosopis juliflora* var. *glandulosa* (Torr.) in Texas, USA. *Meloidodera sikhotealiniensis* parasitizes roots of *Betula mandshurica* in Primorsk territory, Russia, and *M. zacanensis* of tejocote trees (*Crataegus mexicana*) in Mexico. Keys to *Meloidodera* spp. are given by Wouts (1985) and Cid del Prado Vera (1991).

**Subfamily Ataloderinae Wouts, 1973**

**syn. Ataloderini Wouts (Coomans, 1979)**

**Cryphoderini Coomans, 1979**

## Diagnosis

Heteroderidae. Female oval or spheroidal, with a short neck, **does not turn into cyst. Vulva terminal or subterminal**; anus near vulva or on vulval lip. Eggs retained in body, or laid. Cuticle generally with a zig-zag pattern, sometimes striated in neck region. Male with or without tail; develops through metamorphosis. Second-stage juvenile with three incisures (four incisures in *Rhizonema*) in lateral field.

## Type genus

*Atalodera* Wouts & Sher, 1971

syn. *Sherodera* Wouts, 1974

*Thecavermiculatus* Robbins, 1978

## Other genera

*Bellodera* Wouts, 1985

*Camelodera* Krall, Shagalina & Ivanova, 1988

*Cryphodera* Colbran, 1966

*Ekphymatodera* Baldwin, Bernard & Mundo-Ocampo, 1989

*Hylonema* Luc, Taylor & Cadet, 1978

*Rhizonema* Cid del Prado Vera, Lownsbery & Maggenti, 1983

*Sarisodera* Wouts & Sher, 1971

**Key to genera of Ataloderinae**

1. Anus at a short distance from posterior vulval lip ..... 2  
    Anus on or close to posterior vulval lip ..... 4
2. Female with a terminal cone ..... 3  
    Female without a terminal cone ..... **Cryphodera**
3. Excretory pore at stylet level; cloacal tubus in male present ..... **Bellodera**



- Excretory pore behind stylet level; cloacal tubus in male absent ..... *Camelodera*
4. Anus located on inner side of posterior vulval lip ..... *Sarisodera*  
 Anus located on outside of posterior vulval lip ..... 5
5. Most eggs (or juveniles) retained in body; second-stage juveniles having  
 phasmids with a lens-like structure ..... 6  
 Most eggs (or juveniles) not retained in body; second-stage juveniles having  
 phasmids without a lens-like structure ..... 7
6. Cuticle of female with a lace-like pattern, D-layer present; male tail  
 present ..... *Atalodera*  
 Cuticle of female annulated, D-layer absent; male tail absent ..... *Rhizonema*
7. Anus located 73–140  $\mu\text{m}$  from vulva; feeding induces syncytium  
 ..... *Ekphymatodera*  
 Anus located 16–20  $\mu\text{m}$  from vulva; feeding induces single uninucleate  
 giant cell ..... *Hylonema*

See Table 4 for key to Ataloderinae genera lacking a cyst stage.

### Genus *Atalodera* Wouts & Sher, 1971

syn. *Sherodera* Wouts, 1974

*Thecavermiculatus* Robbins, 1978

(Figs 90, C; 91, A, B, D–L; 93, A–M)

### Diagnosis

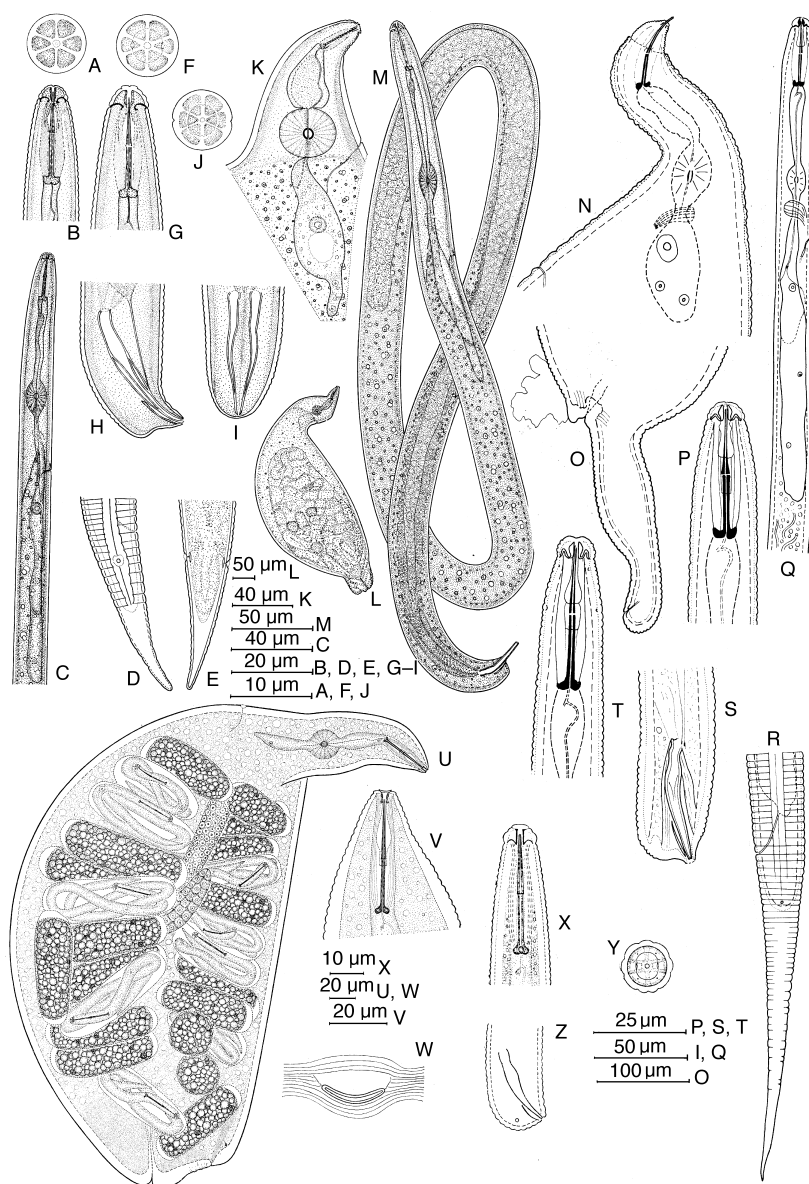
Ataloderinae. **Mature female:** Oval to spheroidal with a projecting neck, 0.36–0.68 mm long, 0.27–0.43 mm wide in type species, young female elongate-obese. **Eggs retained in body**, together with hatched juveniles. **No cyst stage.** Vulva on pronounced terminal flattened cone; **anus on posterior vulval lip. No fenestration around vulva or anus.** Cuticle with a lace-like surface pattern, not annulated, except in anterior region; **D-layer present.** Stylet 26–32  $\mu\text{m}$  long in type species. Vulva terminal or subterminal. Anus near to or at some distance from vulva. **Male:** Slender, under 1.5 mm long (1–1.4 mm in type species), posterior region twisted. Lateral field with four incisures. Cephalic region offset, annulated; basal annule not indented; labial disc present. Stylet longer than in juveniles; 24–29  $\mu\text{m}$  long in type species. Oesophageal glands fill ventral half of body width. Tail cloacal tubus short. Spicules large, over 30  $\mu\text{m}$  long (34–37  $\mu\text{m}$  long, in type species). Phasmids not seen. **Second-stage juvenile:** Body about 0.45–0.56 mm long. Lateral field with three incisures. Cephalic region annulated; labial disc indistinct. Stylet less than 30  $\mu\text{m}$  long (23–25  $\mu\text{m}$  in type species). Oesophageal glands ventral to intestine, filling or not filling body cavity width. Tail conical, terminal hyaline part about half its length. Phasmid with a lens-like structure in or under muscle layer. **Feeding incites a syncytium.**

### Type species

*Atalodera ucrici* Wouts & Sher, 1971

**Table 4.** Key to Ataloderinae genera lacking a cyst stage (modified after de Souza & Huang, 1994).

	<i>Cryphodera</i>	<i>Hylonema</i>	<i>Rhizonema</i>	<i>Ekphymatodera</i>	<i>Bellodera</i>	<i>Camelodera</i>	<i>Sarisodera</i>	<i>Atalodera</i>
Cuticle pattern	Striated	Lace-like	Striated	Tuberculated	Pitted/striated	Smooth	Lace-like	Lace-like
Vulva	Terminal, flush with body	Terminal, flush with body	Terminal, on cone	Terminal, on protuberance	Terminal, on cone	Terminal on cone	Terminal, sunken	Subterminal, on cone or flush
Vulva–anus distance	38–70 µm	16–20 µm	15–33 µm	73–140 µm	53–88 µm	44–85 µm	15 µm	7–91 µm
D-layer	Absent	No data	Absent	No data	Absent	No data	Present	Present
Ex. pore level	Shoulder	Shoulder	Shoulder	Shoulder	Stylet base	Shoulder	Shoulder	Shoulder
Spicules	21–31 µm	27–37 µm	22–34 µm	34–46 µm	22–31 µm	31–37 µm	33–46 µm	23–44 µm
Cloacal tubus	Absent	Present	Present	Present	Present	Absent	Present	Present
Phasmids in J <sub>2</sub>	Lens-like	Pore-like	Lens-like	Pore-like	Lens-like	Pore-like	Lens-like	Lens-like
Feeding site	Giant cell	Giant cell	Giant cell	Syncytium	Giant cell	No data	Giant cell	Syncytium



**Fig. 93.** A–M. *Atalodera ucrici* Wouts & Sher. N–T. *Hylonema iworense* Luc, Taylor and Cadet. U–Z. *Cryphodera eucalypti* Colbran. A and F. *En face* views of juvenile and male, respectively. B and P. Head ends of second-stage juveniles. C and Q. Oesophageal regions of second-stage juveniles. D, E and R. Tail ends of second-stage juveniles. G, T and X. Head ends of males. H, I, S and Z. Tail ends of males. J and Y. *En face* views of males. K, N and V. Head ends of females. L and U. Females. M. Male. O. Postvulval region of an aberrant female. W. Pattern of striations around vulva. (A–M. After Wouts and Sher (1971), courtesy *Journal of Nematology*. N–T. After Luc *et al.* (1978), courtesy *Revue de Nématologie*. U–Z. After Colbran (1966), courtesy *Queensland Journal of Agricultural and Animal Sciences*.)

### Other species

- Atalodera andina* (Golden, Franco, Jatala & Astogaza, 1983) de Souza & Huang, 1994  
 syn. *Thecavermiculatus andinus* Golden, Franco, Jatala & Astogaza, 1983  
*Dolichodera andina* (Golden *et al.*, 1983) Wouts, 1985  
*A. carolynae* (Robbins, 1986) de Souza & Huang, 1994  
 syn. *Thecavermiculatus carolynae* Robbins, 1986  
*A. crassicrustata* (Bernard, 1981) de Souza & Huang, 1994  
 syn. *Thecavermiculatus crassicrustatus* Bernard, 1981  
*A. festucae* Baldwin, Bernard & Mundo-Ocampo, 1989  
*A. gibbosa* de Souza & Huang, 1994  
*A. gracilancea* (Robbins, 1978) de Souza & Huang, 1994  
 syn. *Thecavermiculatus gracilancea* Robbins, 1978  
*A. loniceriae* (Wouts, 1974) Luc, Taylor & Cadet, 1978  
 syn. *Sherodera loniceriae* Wouts, 1974  
*A. trilineata* Baldwin, Bernard & Mundo-Ocampo, 1989

### Note

De Souza and Huang (1994) synonymized *Thecavermiculatus* Robbins, 1978 to *Atalodera* Wouts & Sher, 1971.

ETYMOLOGY. From the Greek *atalos* = tender, and *deras* = skin, ending modified into a Latin feminine, as in *Heterodera*.

The type species was found in soil around roots of *Haplopappus palmari* Gray in the University of California Campus, Riverside, California, USA. *Atalodera gracilancea* was also found in California as a parasite of rattail fescue, *Festuca myuros*, USA. *Atalodera andinus* parasitizes *Capsella bursa-pastoris*, *Chenopodium quinoa*, *Lupinus mutabilis*, *Malvastrum coromandelica*, *Medicago hispida*, *Oxalis tuberosa*, *Solanum tuberosum* subsp. *andigena* and *Ullucus tuberosus* in the Andes mountains, southern Peru. Species of *Atalodera* are similar to *Heterodera* in inducing multinucleate giant cells (syncytia).

### Genus *Cryphodera* Colbran, 1966

syn. *Zelandodera* Wouts, 1973

(Figs 90, B; 93, U–Z)

### Diagnosis

Ataloderinae. **Mature female:** Oval, 0.3–0.6 mm long, 0.15–0.29 mm wide, with a distinct neck usually bent laterally. **No cyst stage;** eggs retained in body. Vulva terminal, lips low to slightly protruding; **no terminal cone.** Anus subterminal, dorsal, **at some distance** (45–70  $\mu\text{m}$  in type species) **from vulva.** Area between anus and vulva concave or flat. **Cuticle thick, finely annulated** except in vulval region. Labial disc present. Phasmids with a lens-like structure in or below muscle layer. Excretory pore opposite oesophageal glands, 99–169  $\mu\text{m}$  from anterior end. **Male:** Body slender, under 1.5 mm (0.7–1 mm in type species). Lateral field with three or four incisures. Cephalic region offset, with two to three annules, **basal annule longi-**

**tudinally indented**; labial disc present; **lateral sectors smaller than submedians**. Stylet long (29–38  $\mu\text{m}$ ), knobs rounded, 3–5.5  $\mu\text{m}$  across. Spicules arcuate with blunt tip, about 21–31  $\mu\text{m}$  long. Gubernaculum thin, slightly arcuate, 6–10  $\mu\text{m}$  long. Tail hemispherical. **Second-stage juvenile**: Cephalic region offset, with three to four annules; labial disc indistinct. Lateral fields with three incisures. Stylet 25–40  $\mu\text{m}$  long. Oesophageal glands fill body cavity width. Tail conical, hyaline portion over 25  $\mu\text{m}$  long. Phasmids with distinct lens-like structure in or below the muscle layer, feeding induces uninucleate giant cell.

#### Type species

*Cryphodera eucalypti* Colbran, 1966

#### Other species

*Cryphodera brinkmani* Karssen & van Aelst, 1999

*C. coxi* (Wouts, 1973) Luc, Taylor & Cadet, 1978  
syn. *Zelandodera coxi* Wouts, 1973

*C. kalesari* Bajaj, Walia, Dabur & Bhatti, 1989

*C. nothophagi* (Wouts, 1973) Luc, Taylor & Cadet, 1978  
syn. *Zelandodera nothophagi* Wouts, 1973

*C. podocarpi* (Wouts, 1973) Luc, Taylor & Cadet, 1978  
syn. *Zelandodera podocarpi* Wouts, 1973

#### Remarks

*Zelandodera* Wouts was synonymized with *Cryphodera* Colbran by Luc *et al.* (1978) because the position of the anus, shape of the vulval lips, male lateral field incisures and juvenile lip markings were considered unacceptable as generic differences. *Cryphodera* shows some ancestral characters, e.g. cuticular annulation, and has been considered by several workers to be a close relative of *Meloidodera* and hence to belong in the Meloidoderinae. However, Ferris (1979), in her cladistic analysis of the Heteroderidae, did not find a basis for suggesting a common ancestor for *Cryphodera* and *Meloidodera*. Baldwin *et al.* (1983) expressed the need for further study on new characters to clarify the phylogenetic relationship between the two genera and pointed out that species of both genera induce a single uninucleate giant cell in their host and that this similarity might reflect more fundamental shared characteristics. However, single uninucleate giant cells are also induced by *Hylonema ivorense*, *Sarisodera hydrophila* and *Rhizonema sequoiae*.

ETYMOLOGY. From Greek *krypha* = secret, hidden, and *deras* = skin, ending modified into a Latin feminine.

The type species was found on *Eucalyptus major* in Brisbane, Australia. It reproduces on other species of eucalyptus. In New Zealand, *Cryphodera coxi* was found on *Metrosideros robusta* A-Cunn.; *C. nothophagi* and *C. podocarpi* were found parasitizing *Nothophagus solandri* var. *solandri* and *Podocarpus totara*, respectively. Karssen and van Aelst (1999) described *C. brinkmani* parasitizing roots of *Pinus thunbergii* in Japan and gave a key to the species of *Cryphodera*.

**Genus *Sarisodera* Wouts & Sher, 1971**

(Figs 87, A–L; 90, D)

**Diagnosis**

Ataloderinae. **Female and cyst:** Body oval, somewhat lemon-shaped, fully swollen, except for small, usually bent neck, 0.4–0.7 mm long, 0.24–0.48 mm wide. **No cyst stage. Vulva terminal, sunken into cone-like protuberance of body;** lips thick, broadly rounded, slightly elevated but not forming a distinct cone; **anus located on ventral (inner) side of posterior vulval lip.** Cuticle with a lace-like pattern, annulated only anteriorly in stylet region; **D-layer present.** Cephalic region with first annule set off, carrying a labial disc. **Stylet long** (45–56  $\mu\text{m}$ ), knobs 6–9  $\mu\text{m}$  across in type species. Median bulb round to oval, offset from precorpus. Eggs retained in body, maximum about 400. **Male:** Body vermiform, twisted in posterior region, 0.6–1.4 mm long. Cephalic region annulated, slightly set off. Labial disc indistinct, basal annule not indented. Stylet 38–46  $\mu\text{m}$  long in type species, knobs round, anterior surface may be concave. Median bulb oval. Oesophageal glands fill body width, overlap intestine mostly ventrally, about twice body width long. Spicules almost straight, 33–46  $\mu\text{m}$  long. Gubernaculum 9–18  $\mu\text{m}$  long. Tail absent, cloacal aperture terminal, cloacal lips forming a short tube. **Second-stage juvenile:** Cephalic region hemispheroidal, annulated, without labial disc. Cuticle annulated, lateral field with four incisures. Stylet 39–43  $\mu\text{m}$  long; knobs 7–8  $\mu\text{m}$  across and anteriorly flattened in type species. Precorpus constricted immediately anterior to median bulb, latter oval. Oesophageal glands fill the body width, extending over intestine ventrally and laterally; nucleus of dorsal gland larger than those of subventrals. Tail conical, in type species 44–61  $\mu\text{m}$  long, with terminal 26–36  $\mu\text{m}$  hyaline; phasmids 37–50  $\mu\text{m}$  from tail tip, **with a lens-like structure in or beneath the muscle layer. Feeding induces a uninucleate giant cell.**

**Type species***Sarisodera hydrophila* Wouts & Sher, 1971

No other species.

ETYMOLOGY. From Greek *sarisa* = a long Macedonian pike, and *deras* = skin; feminine in gender like *Heterodera*.

The type species was found in soil and roots of willow (*Salix lasiolepis* Benth.) in Riverside County, California, USA (type host and locality). It was also found associated with a fern, *Laurel* sp., *Quercus* sp., and *Lyonothamnus floribundus* Gray, in California, USA.

**Genus *Rhizonema* Cid del Prado Vera, Lownsbery & Maggenti, 1983**

(Fig. 92, M–O)

**Diagnosis**

Ataloderinae. **Mature female:** Oval to spheroidal with a projecting neck and distinct terminal cone. **No cyst stage.** Cuticle annulated; **D-layer and subcrystalline layer absent.** Stylet moderately long. Vulva 15–33  $\mu\text{m}$  from anus, situated on terminal

cone. Eggs and hatched juveniles retained in female body. **Male:** Body twisted in posterior region. Lateral fields with four incisures. **Tail absent, anus almost terminal, lips forming tubus.** Spicules straight, posteriorly directed, 22–34  $\mu\text{m}$  long. **Second-stage juvenile:** Lateral field with four incisures. Oesophageal glands filling body cavity width. Tail conical, pointed, with a long terminal hyaline portion. Phasmid with a lens-like structure. **Feeding incites a single uninucleate giant cell.**

#### Type species

*Rhizonema sequoiae* Cid del Prado Vera, Lownsbery & Maggenti, 1983  
syn. *Sarisodera sequoiae* (Cid del Prado Vera, Lownsbery & Maggenti) Wouts, 1985

*Thecavermiculatus sequoiae* (Cid del Prado Vera, Lownsbery & Maggenti) Siddiqi, 1986

No other species.

#### Note

*Rhizonema* was synonymized to *Sarisodera* and *Thecavermiculatus* by Wouts (1985) and Siddiqi (1986), respectively. Luc *et al.* (1988) reinstated *Rhizonema* on grounds of the presence of vulval cone and D-layer of cuticle, absence of male tail and the ability to incite a single giant cell for feeding.

ETYMOLOGY. The name is derived from *rhizo* = root, and *nema* for nematode.

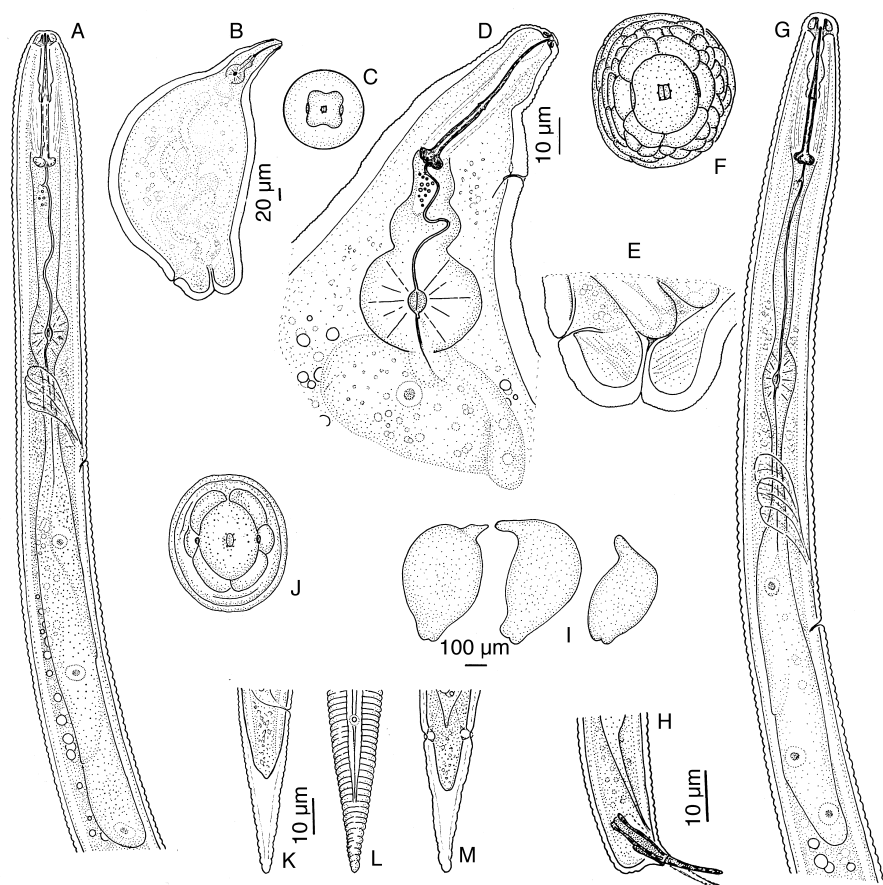
The type species was found parasitizing coast redwood, *Sequoia sempervirens* (D. Don) Endl., growing near Lake Lagunitas, Marin County Water District, California, USA. It was also found on tanbark oak (*Lithocarpus densiflora*), California Bay (*Umbellularia californica*) and Mandrone (*Arbutus menziensis*) in California.

#### Genus *Bellodera* Wouts, 1985

(Fig. 94)

#### Diagnosis

Ataloderinae. **Mature female:** Body spherical, oval or lemon-shaped, with a projecting neck and a **distinct terminal cone**. Cuticle changing colour after death but **no cyst stage**. **Cuticle with irregular transverse striae** and pits between striae; **D-layer absent**; subcrystalline layer present. **Excretory pore at level of base of stylet, 27–56  $\mu\text{m}$  from anterior end.** Vulva a large slit, terminal on a cone which is somewhat flattened. **Anus on slight protuberance on dorsal side of posterior vulva lip, at 53–58  $\mu\text{m}$  from vulva.** **Fenestrae, bullae and underbridge absent.** Eggs retained in body. **Male:** Posterior region of body twisted. Lateral field with four incisures. Stylet of medium strength, 22–31  $\mu\text{m}$  long. Spicules straight, at most 30  $\mu\text{m}$  long, with pointed distal end. Tail short, rounded, anal lips not forming a tube. **Second-stage juvenile:** Lateral field with four incisures. Stylet 35–40  $\mu\text{m}$  long. Oesophageal glands filling body cavity width. Tail elongate-conoid, with hyaline portion about half of its total length. **Phasmids with a lens-like structure.** Feeding incites single uninucleate giant cell.



**Fig. 94.** *Bellodera utahensis* (Baldwin, Mundo-Ocampo & Othman). B–E and I. Mature females. A and J–M. Second-stage juveniles. F–H. Males. A, D and G. Oesophageal regions. B and I. Females. C, F and J. *En face* views. E. Posterior cone region of female showing anus and vulva. H and K–M. Tail ends. (After Baldwin *et al.*, 1983a, courtesy of the *Journal of Nematology*.)

### Type species

*Bellodera utahensis* (Baldwin, Mundo-Ocampo & Othman, 1983) Wouts, 1985  
syn. *Cryphodera utahensis* Baldwin, Mundo-Ocampo & Othman, 1983  
No other species.

### Note

*Bellodera* differs from *Cryphodera* in having females marked by transverse striae and having a terminal cone and the excretory pore located much anterior (at 99–169 µm from anterior end in species of *Cryphodera*).

ETYMOLOGY. Derived from Bell-o = honouring Arnold Bell, and *deras* = skin.

The type species parasitizes wild rose in Utah, USA.



**Genus *Hylonema* Luc, Taylor & Cadet, 1978**

(Fig. 93, N–T)

**Diagnosis**

Ataloderinae. **Mature female:** Swollen, elongate to oval, with a short but distinct projecting neck, usually bent to one side, and a rounded posterior end, 0.34–1.01 mm long, 0.16–3.4 mm wide in type species. **Vulva terminal in a slight depression**, 40–46  $\mu\text{m}$  long; lips not protruding; underbridge present but fenestrae and bullae absent. Anus almost terminal, **on posterior vulval lip, 16–20  $\mu\text{m}$  from vulva** in type species. **No cyst stage. Most eggs not retained in body, but deposited singly in a gelatinous matrix.** Cuticle thick, annulated only in anterior region, behind which with a rugose surface; punctations absent. Cephalic end conoid, cephalic region continuous. Stylet slender, 38–46  $\mu\text{m}$  long. **Male:** Body 0.6–1.4 mm long, twisted in posterior region. Lateral field with four incisures. Cephalic region rounded, offset, annulated; basal annule not indented; labial disc indistinct, in SEM dorsoventrally elongated; framework high arched. Stylet moderately developed, 38–44  $\mu\text{m}$  long in type species. Oesophageal glands elongated, filling width of body, extending over intestine ventrally or ventrolaterally. Spicules moderately thick, bifid at tip, 27–37  $\mu\text{m}$  long in type species. **Tail extremely short, or absent; cloacal lips forming a short tube.** Phasmids not seen. **Second-stage juvenile:** Body 0.6–0.73 mm long. Lateral field with three incisures. Cephalic region rounded, offset, annulated; labial disc indistinct, in SEM dorsoventrally oblong with slit-like amphidial apertures; oral opening small rectangular, lacking inner labial pits around it; labial annule not indented. Stylet moderately developed, 33–40  $\mu\text{m}$  long. Oesophageal glands as in male. Tail elongate-conoid, 77–92  $\mu\text{m}$  long, with 55–88  $\mu\text{m}$  long terminal hyaline portion. Phasmids dot-like, 8–17  $\mu\text{m}$  behind anal level, **without a lens-like structure underneath. Feeding incites a single uni-nucleate giant cell.**

**Type species***Hylonema ivorense* Luc, Taylor & Cadet, 1978

No other species.

ETYMOLOGY. From Greek *hylé* = wood, forest, and *nema* = nematode.

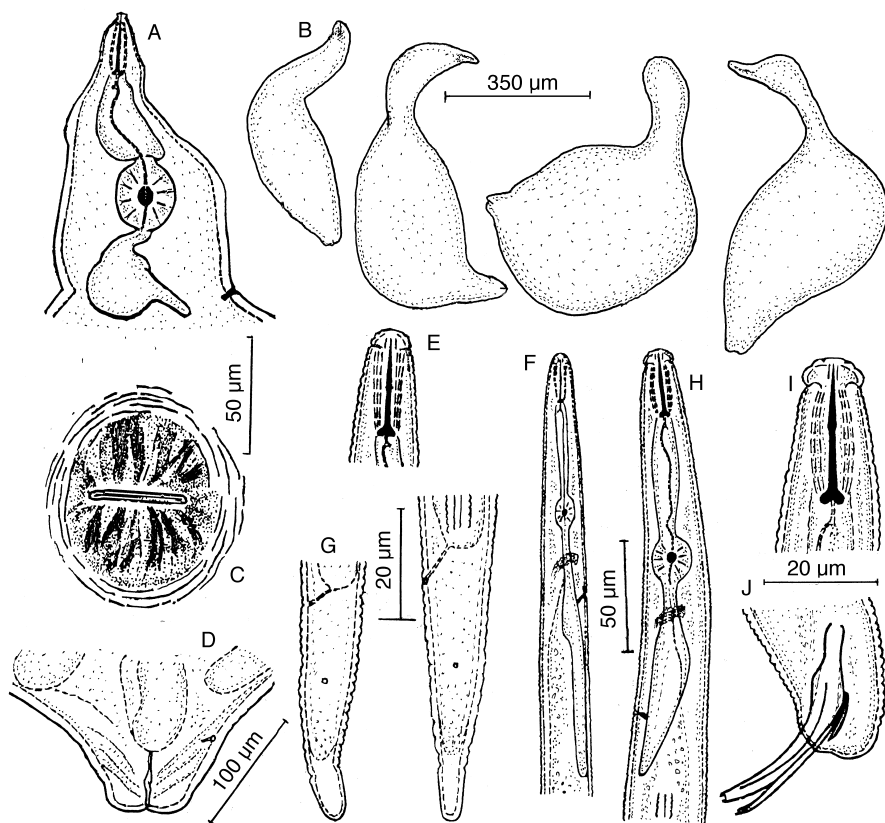
The type species was found parasitizing roots of *Turraeanthus africana* Pellegr. near Abidjan, Côte d'Ivoire.

**Genus *Camelodera* Krall, Shagalina & Ivanova, 1988**

(Fig. 95)

**Diagnosis**

Ataloderinae. **Mature female:** Oval, rounded or irregular in outline, **with a long neck**, 0.39–0.76 (0.6) mm long, 0.22–0.56 (0.4) mm wide. **No cyst stage;** eggs retained in body or deposited in eggsac. Vulva a long slit 39–49 (42)  $\mu\text{m}$ , terminal, lips rounded, protruding; **terminal cone present. Anus located outside vulval cone at some distance (44–85  $\mu\text{m}$ ) from vulva.** Cuticle moderately thick, not



**Fig. 95.** *Camelodera eremophila* Krall, Shagalina & Ivanova. A. Female, anterior region. B. Females. C. Vulva, ventral view. D. Vulval cone showing vulva and anus. E and G. Head end and tail ends of second-stage juveniles, respectively. F and H. Oesophageal region of second-stage juvenile and male, respectively. I and J. Head end and tail end of male, respectively. (Redrawn after Krall *et al.*, 1988.)

annulated, pearly white becoming brownish but remaining elastic. **Stylet short**, 19.5–23.7 (21.6)  $\mu\text{m}$  long in type species. **Male:** Body slender, over 1 mm ( $a = 31\text{--}46$ ;  $L = 1.19\text{--}1.74$  (1.43) mm in type species). Lateral field with three or four incisures. Cephalic region smoothly rounded, distinctly offset by a constriction with a prominent labial disc. Stylet 22.8–24.8 (24)  $\mu\text{m}$  long in type species, with rounded basal knobs. Oesophageal glands about two body widths long, not filling body cavity. Spicules cephalated, ventrally arcuate, 31–37 (34.4)  $\mu\text{m}$  long; terminus with a single notch. Gubernaculum small, fixed. Tail hemispherical. **Second-stage juvenile:** Body 0.34–0.43 (0.37) mm long in type species;  $a = 20\text{--}26$ . **Stylet short** (17.9–18.6 (18.1)  $\mu\text{m}$ ). Cephalic region slightly offset from body, with three annules; labial disc indistinct. Lateral fields with four incisures. Oesophageal glands not filling body width. Tail conical, hyaline portion less than one-third of tail length. Phasmids pore-like, usually just anterior to middle of tail. Tail short ( $c = 8.5\text{--}19.4$ ), tapering to a large smoothly rounded terminal annule, with 15–19 annules.

## Type species

*Camelodera eremophila* Krall, Shagalina & Ivanova, 1988

No other species.

ETYMOLOGY. '*Camelo*' probably from camel-like elongate neck of females, and suffix of *Heterodera*.

The type species was found parasitizing roots of *Calligonum arborescens* Litv. (Polygonaceae) in Yeradzhi Desert Reserve in Kara Kum Desert, 70 km north of Repetek Desert Station in Tshardzou district, eastern Turkmania.

**Genus *Ekphymatodera* Baldwin, Bernard & Mundo-Ocampo, 1989**

(Fig. 96)

## Diagnosis

Ataloderinae: **Mature female:** Swollen, with a short but distinct projecting neck, straight or slightly bent, and a rounded posterior end, 0.51–0.79 (0.63) mm long, 0.21–0.47 (0.33) mm wide. **Vulva terminal, on a broad protuberance with smooth lips**, 40–58 (49.8)  $\mu\text{m}$  long. Anus distinct, terminal, **on posterior vulval lip**, **73–140 (96.2)  $\mu\text{m}$  from vulva**. **No cyst stage**. Cuticle surface with minute tubercles, irregular longitudinal striae superimposed over tubercles anastomosing near posterior terminus. Labial disc squarish; lip areas fused to form a plate-like annule. Stylet slender, 32–35.5 (33.4)  $\mu\text{m}$  long in type species. Excretory pore near level of dorsal gland nucleus, 94–178 (129.2)  $\mu\text{m}$  from anterior end. **Male:** Body 1.07–1.65 (1.42) mm long in type species, twisted in posterior region by 90°. Lateral field with four incisures, areolated towards extremities. Cephalic region rounded, slightly offset, with five to seven annules in type species. In SEM lips fused with one another and with labial disc, lateral lips partially separate. Stylet moderately developed, 26.3–33.7 (29.8)  $\mu\text{m}$  long in type species. Oesophageal glands short, not filling width of body. Spicules moderately thick, bifid at tip, 34.0–45.5 (38.6)  $\mu\text{m}$  long in type species. **Tail extremely short, or absent; cloacal lips forming a short tubus**. Phasmids not seen. **Second-stage juvenile:** Body 0.56–0.75 (0.63) mm long in type species. Lateral field with four incisures, areolated. Cephalic region rounded, slightly offset, annulated; adjacent submedian lips fused with one another and labial disc; lateral lips fused with labial disc but not with submedian lips. Stylet moderately developed, 28–32 (30)  $\mu\text{m}$  long in type species. Oesophageal glands filling body cavity width. Tail elongate, much tapering in posterior half, 76–110 (98.4)  $\mu\text{m}$  long, with 60–103 (69)  $\mu\text{m}$  long terminal hyaline portion. Phasmidial opening pore-like, duct cuticularized. **Feeding incites a syncytium**.

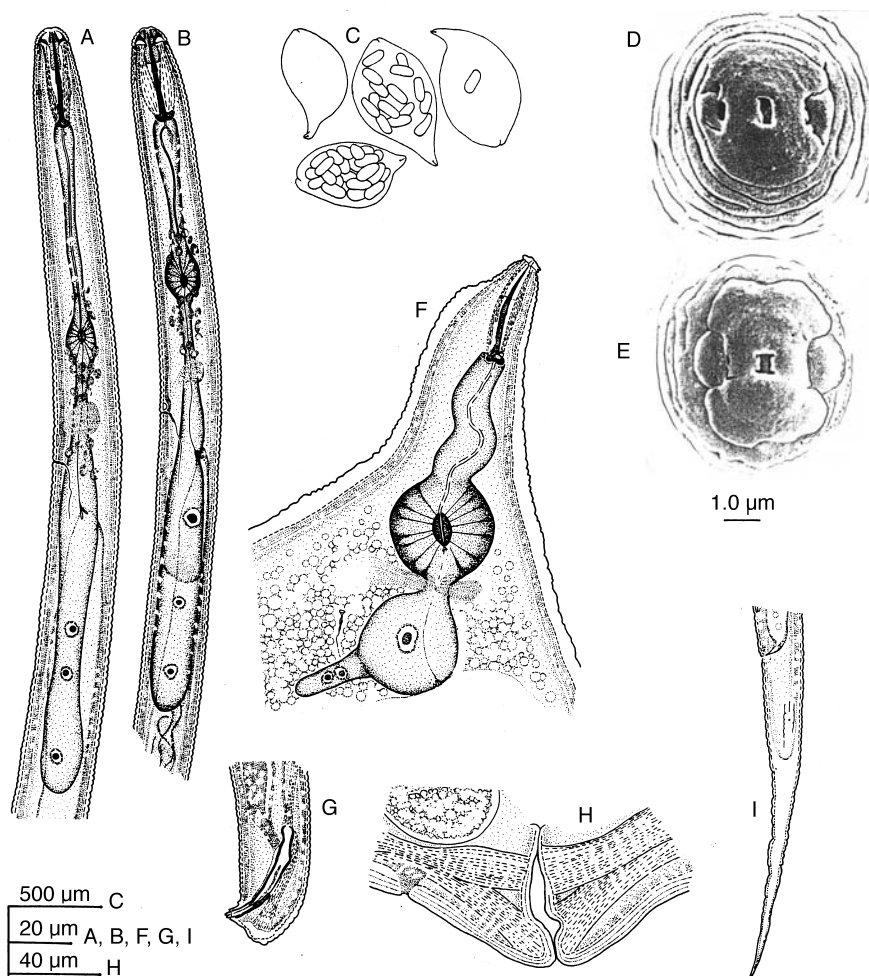
## Type species

*Ekphymatodera thomasoni* Baldwin, Bernard & Mundo-Ocampo, 1989

No other species.

## Remarks

*Ekphymatodera* is very similar to *Hylonema* but differs from it in its female cuticular pattern and having a much greater vulva–anus distance. Unlike *Hylonema*, it induces a syncytium at its feeding site. *Ekphymatodera thomasoni* induces a poorly



**Fig. 96.** *Ekphymatodera thomasoni* Baldwin, Bernard & Mundo-Ocampo, 1989. A. Oesophagus of male. B. Oesophagus of second-stage juvenile. C. Females. D. *En face* view of male. E. *En face* view of second-stage juvenile. F. Anterior end of female. G. Posterior end of male. H. Vulval-anal region. I. Tail end of second-stage juvenile. (After Baldwin *et al.*, 1989, courtesy of the *Journal of Nematology*.)

defined syncytium on *Carex* and *Juncus* hosts which is intermediate between the thick-walled single uninucleate giant cell of *Sarisoderini* and the large multinucleate syncytia lacking wall ingrowths of *Ataloderini* (Mundo-Ocampo & Baldwin, 1992).

**ETYMOLOGY.** From Greek *ekphymatos* = eruption of pimples and *deras* = skin, referring to unique cuticular surface pattern of females.

The type species was collected from roots and soil of *Juncus effusus* L. var. *pacificus*, from a meadow on the south bank of Merced River in Yosemite Valley, Yosemite National Park, California, USA.

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# VII Superfamily Dolichodoroidea

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## SUPERFAMILY DOLICHODOROIDEA CHITWOOD IN CHITWOOD & CHITWOOD, 1950 (SIDDIQI, 1986)

### Diagnosis

Hoplolaimina. Juveniles and adults vermiform; **mature female not obese**. No **marked sexual dimorphism in anterior region**. Cuticle prominently annulated, not showing distinct outer and inner layers (except Merliniinae). Lateral fields each with one to six incisures (one incisure only in *Belonolaimus*), number reducing towards extremities. Deirids present only in Merliniinae and Psilenchidae. Amphidial apertures pore-like or oval slits, usually near labial sensilla, or near cephalic sensilla. **Phasmids small with pore-like aperture, on tail** or just preanal as in females of some species of *Neodolichodorus* which have short hemispherical tails, **in males extending into bursa, forming a pair of pseudoribs**. Cephalic framework mostly with high arches and conspicuous extensions projecting posteriorly, with light to heavy sclerotization; annules generally distinct, **basal annule mostly not indented**. Labial disc prominent in Dolichodoridae and in some members of Telotylenchinae which have long stylets. Oral aperture small, round or oval, **surrounded by six labial sensilla**. Stylet long (over 100  $\mu\text{m}$ ) to short (about 10–12  $\mu\text{m}$ ), with distinct basal knobs (knobs absent in Psilenchidae). Orifice of dorsal oesophageal gland near stylet base. Corpus with cylindrical precorpus (= procorpus) and **a muscular round to oval postcorpus** (= metacorpus) **having refractive cuticular thickenings**. Isthmus slender. **Basal (terminal) oesophageal bulb enclosing oesophageal glands present, or only the dorsal gland enlarging and extending over anterior end of intestine, while subventral glands remaining small and anterior to the dorsal gland and may or may not overlap intestine**. **Oesophago-intestinal valve or cardia three-celled, well developed**, but reduced in forms with overlapping glands. Intestine with indistinct cell walls and lumen, containing refractive food globules, and in several genera with serpentine canal-like fasciculi, may form a postrectal sac in some genera. **Female reproductive system didelphic, amphidelphic**, secondarily

becoming pseudo-mono-prodelphic by the reduction of the posterior branch in *Trophurus*. Vulva a transverse slit, rarely round or oval, median or postmedian, with or without epitygma; **lateral vulval membranes absent**. Vagina at right angles to body axis, sclerotized in Dolichodorinae. Glandular distal part of uterus (= crustaformeria) tricolomellate. Spermathecae axial, round (in most groups), lobed (Merliniinae) or sac-like (Psilenchidae). Ovaries outstretched, oocytes in one row except in region of multiplication. **Female tail rarely less than two anal body widths long**, variously modified being conoid, cylindroid, subclavate or elongate-filiform. Male monorchic, with outstretched testis; sperm small to moderately large, rounded, with little cytoplasm. Bursa enveloping entire tail or, in Psilenchidae, adanal. Spicules symmetrical, cephalated, ventrally arcuate, with distal flanges (vela) and pointed tip bearing subterminal pore or cylindroid with tip broadly rounded and notched (Merliniinae). **Gubernaculum** simple or modified, fixed or protrusible, **without titillae and telamon** (= capitulum). Cloacal lips not modified into a penial tube. Hypopygium (cloacal lip papillae) usually not visible (except in Merliniinae). Juveniles essentially similar to female. **Obligate migratory ectoparasites of roots.**

#### Type family

Dolichodoridae Chitwood in Chitwood & Chitwood, 1950

#### Other families

Belonolaimidae Whitehead, 1960 (Siddiqi, 1970)

Psilenchidae Paramonov, 1967

Telotylenchidae Siddiqi, 1960

#### Remarks

Dolichodoroidea differs from Hoplolaimoidea in having subventral oesophageal glands not enlarged or extending past the dorsal gland, while the male cephalic region, stylet and oesophagus are similar to those in the female and do not show marked sexual dimorphism (Fig. 13). Members of the family Psilenchidae show some resemblances to those of the Tylenchidae, particularly the weak stylet and elongate tail, but the presence of phasmids in the middle of the lateral fields in the tail region and didelphy easily differentiate them.

#### Key to families of Dolichodoroidea

1. Tails similar between sexes, generally filiform; bursa adanal ..... **Psilenchidae**  
Tails dissimilar between sexes, not filiform (except terminally only in some Dolichodoridae); bursa enveloping entire tail ..... 2
2. Cephalic region generally four-lobed with reduced lateral lip areas; basal plate strongly sclerotized; vaginal wall usually sclerotized; stylet conus often much longer than shaft ..... 3  
Cephalic region rounded, not four-lobed, lateral lip areas not reduced; basal plate or vaginal wall not strongly sclerotized; stylet conus usually about as long as shaft (except Macrotrophurinae) ..... **Telotylenchidae**

3. Oesophageal glands not overlapping intestine; oesophago-intestinal junction more than two body widths from median bulb; bursa trilobed .... **Dolichodoridae**  
Oesophageal glands overlapping intestine; oesophago-intestinal junction about one body width from median bulb; bursa simple, not trilobed..... **Belonolaimidae**

## FAMILY DOLICHODORIDAE

### (The awl nematodes)

This family comprises migratory ectoparasites of roots which are known as awl nematodes since they have very long stylets. Most of these nematodes are deep root tissue feeders and can subsist on a variety of host plants. Long stylet-bearing *Dolichodorus* spp. occur in forest soil, near streams and rivers and in cultivated land in North and South America, Italy, India, Nigeria, Togo, New Caledonia and the Philippines (Kleynhans *et al.*, 1996). *Dolichodorus longicaudatus* causes stunting, chlorosis and reduced clipping weights of *Mentha spicata* (Rhoades, 1983). *Dolichodorus heterocephalus* severely damages root systems and reduces the yield of maize and celery in Florida and is damaging to maize, tomato and pepper. These nematodes prefer lighter soils and their activity is highest at soil temperatures between 25 and 30°C. *Neodolichodorus* spp. are distributed in North and South America, Africa, Australia, New Zealand and Europe. *Neodolichodorus brevistilus* occurs on sugarcane in South Africa.

*Dolichodorus obtusus* Allen was designated, almost simultaneously, as the type species of new genera *Neodolichodorus* and *Plesiodorus* by Andr  ssy (1976) and Siddiqi (1976), respectively and thus these genera are objective synonyms; *Neodolichodorus*, having 22 days' priority in publication, is the valid generic name.

*Dolichodorus*, with a four-lobed head, has a longitudinally oval-appearing amphidial aperture but *Neodolichodorus* has a transversely oval amphidial aperture; the presence of a quadricolumella in these genera, including *Dolichodorus*, is disputable. The glandular region of the uterus in the entire group, including Dolichodorinae, Telotylenchinae and Belonolaiminae, is of the same pattern, i.e. a tricolumella (see Geraert, 1983), in which the three rows of cells are often not straight but staggered and the region shows three cells in a cross-section. *Dolichodorus* spp. that I have studied do have a tricolumella, with staggered columns of cells. The elongate, terminally filiform tail and a trilobed bursa, as seen in *Dolichodorus* and *Brachydorus*, are similar to *Meiodorus* but the latter lacks cephalic sclerotization, a labial disc and vaginal sclerotization and thus comes close to telotylenchids.

Maggenti *et al.* (1987) restricted the Dolichodoridae to *Dolichodorus* and *Neodolichodorus* and recognized the Belonolaimidae with Belonolaiminae and Telotylenchinae. Under Telotylenchinae, they included, besides others, *Merlinius*, *Amplimerlinius* and *Nagelus*, and assigned *Geocenamus* and *Macrotrophurus* to Belonolaiminae and Tylenchidae (Tylenchidae), respectively. Fortuner & Luc (1987) reviewed the family Belonolaimidae and differentiated it from Dolichodoridae by the glandular part of the uterus having three rows of cells as against four rows in the latter. This differentiation is invalid since *Dolichodorus* spp. have a tricolumella. Luc

& Fortuner (1987) stressed the importance of the strong sclerotization of the basal plate and arches of the cephalic framework in support of recognizing Dolichodoridae as different from Belonolaimidae.

The longitudinally oval amphidial slit, the tricolumella/quadricolumella and the cephalic framework sclerotization, as seen in the three genera (*Dolichodorus*, *Neodolichodorus* and *Brachydorus*) presently included in Dolichodoridae by Maggenti *et al.* (1987) and Luc & Fortuner (1987), can be used for characterizing the subfamily Dolichodorinae. To show the inter-relationship of various groups of dolichodorids, one may either follow Siddiqi's (1986) classification of Dolichodoroidea with several subfamilies of equal status under Dolichodoridae, or recognize Dolichodoridae, Meiodoridae, Telotylenchidae, Macrotrophuridae, Merliniidae and Belonolaimidae under Dolichodoroidea, which action would be inflationary at the family level. Here I propose a middle way of classifying Dolichodoroidea as having four families – Dolichodoridae, Belonolaimidae, Telotylenchidae and Psilenchidae.

*Brachydorus* was proposed by de Guiran & Germani (1968) in the Dolichodorinae and characterized by a trilobed bursa, a filiform female tail mostly comprising a hyaline part, a heavily sclerotized cephalic framework, a robust but relatively short stylet and a smooth cephalic region not divided into four lobes. Siddiqi (1986) assigned it to the Meiodorinae of the Dolichodoridae. The amphidial apertures of *Meiodorus* are probably pore-like facing anteriorly and of *Brachydorus* large oblique slits. These genera have a circular or hexagonal cephalic region, elongate-tapering tail and trilobed bursa. *Brachydorus* has a strongly sclerotized basal plate of the cephalic framework and vaginal wall but has a relatively shorter stylet than members of the Dolichodorinae. A separate subfamily, Brachydorinae subfam. n., for this genus seems justified. Luc & Fortuner (1987) proposed *Brachydorus* as a genus *dubium* since it lacked information on the morphology of the face, but it was later recognized as a valid genus by Maggenti *et al.* (1988).

## Family Dolichodoridae Chitwood in Chitwood & Chitwood, 1950 (Skarbilovich, 1959)

### Diagnosis

Dolichodoroidea. Small to large sized (generally about 1.0–1.5 mm), straight, usually arcuate, or more curved. Cuticle strongly annulated. Lateral fields each with three to four incisures. Phasmids pore-like, caudal. Cephalic region usually **four-lobed; labial disc usually distinct. Basal plate and arches of the cephalic framework strong sclerotized.** Amphidial apertures longitudinal or dorsoventral slit-like. Stylet well developed, usually very long. **Oesophageal glands enclosed in a basal bulb abutting intestine.** Oesophago-intestinal junction more than one corresponding body width from median bulb. Didelphic, amphidelphic. Vulva median or submedian, transverse slit-like. **Vaginal wall sclerotized.** Spermathecae axial, rounded. **Postrectal intestinal sac present. Tails dissimilar between sexes:** female tail elongate, usually filiform with spicate tip, or hemispherical to mamillate (*Neodolichodorus*). Male tail short, conoid, completely enveloped by a bursa which is trilobed having two large lateral lobes and a small terminal lobe. Spicules well developed, similar, pointed, with or without distal flanges. Gubernaculum usually large, protrusible. Hypopygium absent. Migratory deep root tissue feeders.



## Type subfamily

Dolichodorinae Chitwood in Chitwood & Chitwood, 1950

## Other subfamily

Brachydorinae subfam. n.

**Key to subfamilies of Dolichodoridae**

1. Cephalic region four-lobed; labial disc distinct; stylet 50–170  $\mu\text{m}$   
     long ..... **Dolichodorinae**
- Cephalic region not four-lobed; labial disc indistinct; stylet under 40  $\mu\text{m}$   
     long..... **Brachydorinae**

**Subfamily Dolichodorinae Chitwood in Chitwood & Chitwood, 1950**

## Diagnosis

Dolichodoridae. Large sized (1.5–3 mm). Lateral field with three to four incisures, areolated. **Cephalic region offset, distinctly four-lobed, framework and basal plate strongly sclerotized; labial disc distinct; stylet strong, elongate (over 50  $\mu\text{m}$ ) with conus markedly longer than shaft, and prominent knobs. Intestinal fasciculi and postrectal sac present. Vaginal wall sclerotized.** Ovaries paired. Female and juvenile tails long, filiform to spicate or, if obtuse to mamillate, then less than two anal body widths long and with annulated terminus. **Male tail short, conical; bursa trilobed** with two large flap-like lateral lobes and a small terminal lobe; spicules with or without distal flanges; gubernaculum large, usually protrusible.

## Type genus

*Dolichodorus* Cobb, 1914

## Other genus

*Neodolichodorus* Andr  ssy, 1976

**Key to genera of Dolichodorinae**

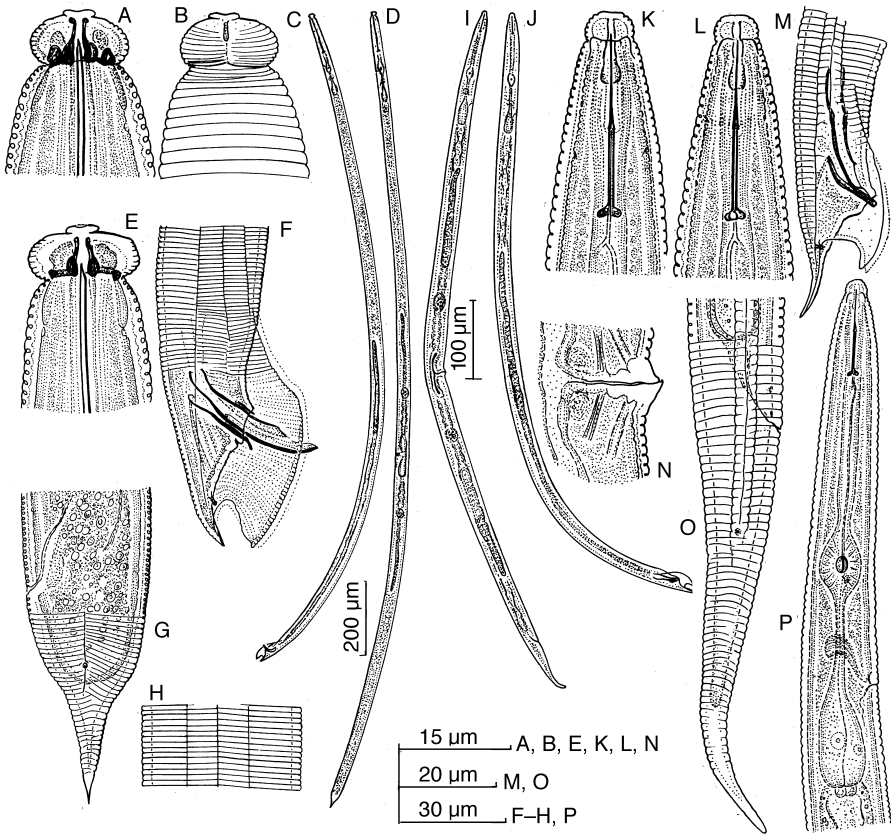
1. Lateral field with three incisures; female tail spicate or filiform ..... ***Dolichodorus***
- Lateral field with four incisures; female tail obtuse or  
     mamillate ..... ***Neodolichodorus***

**Genus *Dolichodorus* Cobb, 1914**

(Figs 11, C & D; 97, A–H)

## Diagnosis

Dolichodorinae. Body straight to arcuate when relaxed. **Lateral field with three incisures**, completely areolated. Phasmids just postanal. Amphidial apertures small, longitudinal slits confined to the front region of **cephalic region, which is prominently four-lobed; labial disc conspicuous, large. Sclerotization of basal plate of framework massive.** Stylet exceptionally elongate (50–170  $\mu\text{m}$ ), stylet guide (stoma) elongate-tubular. Precorpus swollen with convoluted lumen when stylet is retracted. Median and basal bulbs well developed, joined by a short slender isthmus.



**Fig. 97.** A–H. *Dolichodorus heterocephalus* Cobb. I–P. *Meiodorus hollisi* Siddiqi. A, B and K. Head ends of females. C and J. Males. D and I. Females. E and L. Head ends of males. F and M. Tail ends of males. G and O. Tail ends of females. H. Lateral field. N. Vulval region. P. Oesophageal region of female. (A–P. After Siddiqi (1976), courtesy *Nematologica*.)

Excretory pore well anterior to hemizonid. Vulval lips not modified. **Vaginal sclerotization in lateral view symmetrical. Female tail convex-conoid anteriorly, then conoid-spicate to filiform**, more than one and a half anal body widths long except *D. cobbi*, which has a tail about one anal body width long, since tail projection is very small. Postrectal intestinal sac only filling convex-conoid region of tail. Bursa large, trilobed. Spicules robust, with large flanges; gubernaculum also robust, protrusible.

#### Type species

*Dolichodorus heterocephalus* Cobb, 1914

#### Other species

*Dolichodorus aestuarius* Chow & Taylor, 1978

*D. aquaticus* Doucet, 1986

- D. cobbi* Golden, Handoo & Wehunt, 1986  
*D. grandaspicatus* Robbins, 1982  
*D. kishansinghi* Jairajpuri & Rahmani, 1979  
*D. longicaudatus* Doucet, 1981  
*D. marylandicus* Lewis & Golden, 1981  
*D. minor* Loof & Sharma, 1975  
*D. miradvulvus* Smart & Khuong, 1985  
*D. nigeriensis* Luc & Caveness, 1963  
*D. pellegrini* Germani, 1990  
*D. profundus* Luc, 1960  
*D. pulvinus* Khan, Seshadri, Weischer & Mathen, 1971  
*D. silvestris* Gillespie & Adams, 1962  
*D. similis* Golden, 1958

ETYMOLOGY. From Greek *dolichos* = long, and *dory* = spear.

The type species (male) was collected from fresh water, Douglas Lake, Michigan, and (female) from Silver Spring, Florida, USA. Keys to species have been provided by Lewis and Golden (1981), Smart and Khuong (1985) and Esser (1989).

### Genus *Neodolichodorus* Andr ssy, 1976

syn. *Plesiodorus* Siddiqi, 1976

(Fig. 98, A–G)

#### Diagnosis

Dolichodorinae. **Body strongly curved or arcuate upon relaxation. Lateral field with four incisures.** Phasmids adanal, just preanal or just postanal. Amphidial apertures small, dorso-ventral slits. **Cephalic region annulated or smooth, offset, not prominently lobed;** labial disc present, generally not prominent. Cephalic framework strongly sclerotized. Stylet exceptionally elongate (50–140  $\mu\text{m}$ ), with conus longer than the shaft; stylet guide elongate, tubular. Precorpus cylindrical or swollen; median and basal bulbs well developed. Excretory pore anterior to hemizonid. Vulval lips usually modified, anterior one projecting posteriorly. **Vaginal sclerotization in lateral view asymmetrical. Female tail short,** less than two anal body widths long, obtusely rounded or mamillate, with annulations following its contour (rarely spicate as in *N. rageshi*); terminal tail cuticle not abnormally thickened. Postrectal intestinal sac filling most of tail cavity. Juvenile tails also obtusely rounded, but the early-stage juvenile of the type species has a spicate tail. Male tail short, bursa large, trilobed. Spicules slender, with a small knob-like tip, not prominently flanged. Gubernaculum large, slender, apparently non-protrusible.

#### Type species

*Neodolichodorus obtusus* (Allen, 1957) Andr ssy, 1976

syn. *Dolichodorus obtusus* Allen, 1957

*Plesiodorus obtusus* (Allen) Siddiqi, 1976

(*Dolichodorus obscurus* in Allen, 1957 = *lapsus calami*)

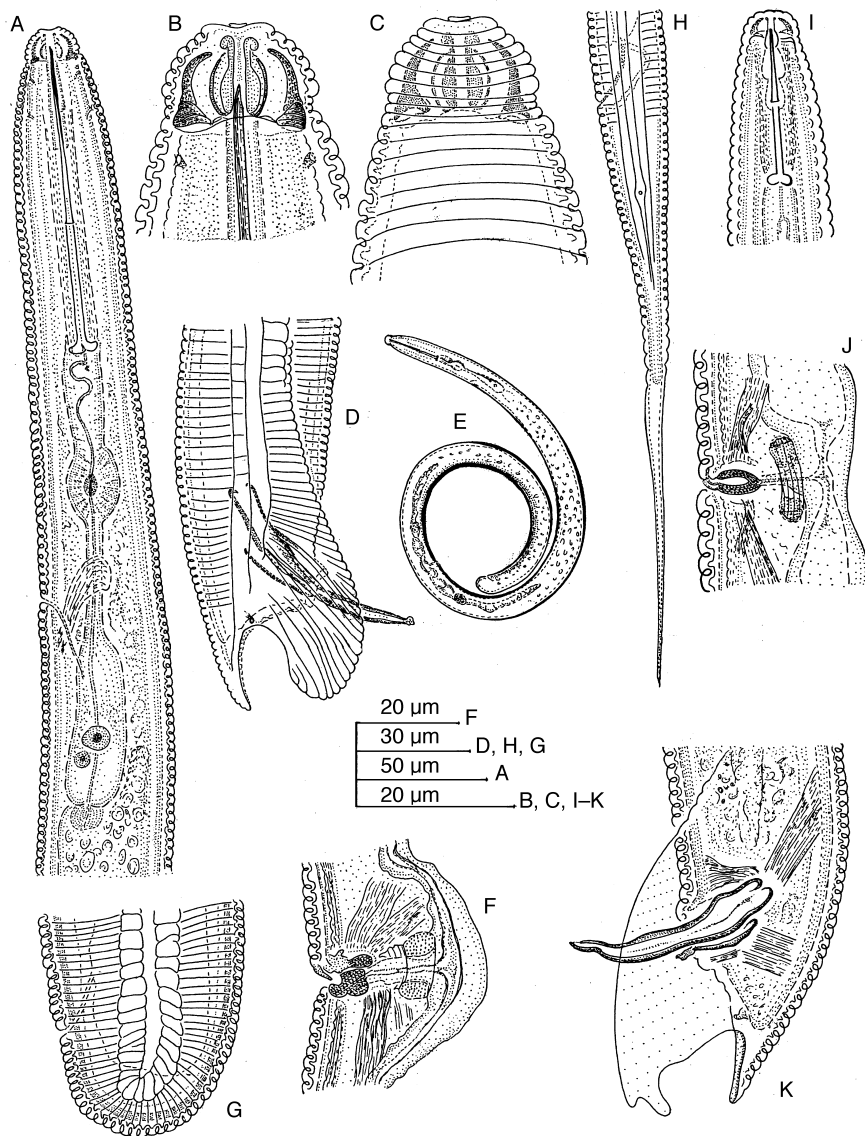


Fig. 98. A–G. *Neodolichodorus obtusus* (Allen), paratypes. H–K. *Brachydorus tenuis* de Guiran & Germani, paratypes. A. Oesophagus of female. B and C. Head ends of female. D and K. Tail ends of male. E. Entire female. F and J. Vulval regions. G and H. Tail ends of female. I. Head end of male.

#### Other species

*Neodolichodorus adelaidensis* (Fisher, 1964) Siddiqi, 1977

syn. *Dolichodorus adelaidensis* Fisher, 1964

*Plesiiodorus adelaidensis* (Fisher) Siddiqi, 1976

- N. arenarius* (Clark, 1963) Siddiqi, 1977  
 syn. *Dolichodorus arenarius* Clark, 1963  
*Plesiodorus arenarius* (Clark) Siddiqi, 1976
- N. brevistilus* (Heyns & Harris, 1973) Siddiqi, 1977  
 syn. *Dolichodorus brevistilus* Heyns & Harris, 1973  
*Plesiodorus brevistilus* (Heyns & Harris) Siddiqi, 1976
- N. cassati* (Luc & Dalmasso, 1971) Siddiqi, 1977  
 syn. *Dolichodorus cassati* Luc & Dalmasso, 1971  
*Plesiodorus cassati* (Luc & Dalmasso) Siddiqi, 1976
- N. citri* s'Jacob & Loof, 1996
- N. leioccephalus* Doucet, 1981
- N. paralongicaudatus* Rashid, Geraert & Heyns, 1990
- N. rageshi* sp. nov.  
 syn. *Neodolichodorus* spec. apud Rashid, Geraert & Sharma (1987)
- N. rostrulatus* (Siddiqi, 1976) Siddiqi, 1977  
 syn. *Plesiodorus rostrulatus* Siddiqi, 1976

### Remarks

*Plesiodorus* Siddiqi is a junior objective synonym of *Neodolichodorus* Andr ssy being based on the same type species and published 22 days after *Neodolichodorus* (see Siddiqi, 1977). A somewhat similar event occurred when Jairajpuri (1984a) found the publication dates of *Divittus* Jairajpuri, 1984 and *Morasinema* Javed, 1984 to have fallen on the same day, and following ICZN Article 24, as 'first reviser', chose the former as a valid name, since the two names are objective synonyms of each other. *Neodolichodorus* spec. apud Rashid, Geraert & Sharma (1987) is here given a new name, *Neodolichodorus rageshi* which is described, illustrated and differentiated from related species by Rashid *et al.* (1987).

ETYMOLOGY. Greek *neos* = young, new, and *Dolichodorus*.

The type species was collected from the soil around the roots of *Aretostaphylos man-zahita* Parry in Napa County, California, USA.

## Subfamily Brachydorinae subfam. n.

### Diagnosis

Dolichodoridae. **Lateral field with four incisures, not areolated on most of body. Cephalic region rounded, offset; labial disc indistinct; framework heavily sclerotized; amphidial apertures slit-like, obliquely or dorso-ventrally placed on head. Stylet slender or robust, not very long**, with tubular conus slightly longer than the shaft and prominent, rounded basal knobs. Precorpus elongate-slender. Median bulb not set off from precorpus, with large oval refractive thickenings. **Vagina sclerotized**. Spermathecae round or oval. Ovaries outstretched. **Female tail elongate-filiform** to an attenuated tip, hyaline portion more than half tail length. Phasmids on tail. Male tail short, conical, enclosed in a trilobed bursa; lateral lobes of bursa large. Spicules apparently not flanged. Gubernaculum robust, trough-shaped.

## Type genus

*Brachydorus tenuis* de Guiran & Germani, 1968

No other genus.

**Genus *Brachydorus* de Guiran & Germani, 1968**

(Fig. 98, H–K)

## Diagnosis

Brachydorinae. **Lateral field with four incisures, not areolated on most of body.** Cephalic region rounded, **non-annulated; framework heavily sclerotized;** labial disc indistinct; **amphidial apertures slit-like, obliquely or dorso-ventrally placed on head.** Stylet 19–35  $\mu\text{m}$  long, with tubular conus slightly longer than the shaft and prominent, rounded basal knobs. Precorpus elongate-slender. Median bulb not set off from precorpus, with large oval refractive thickenings. Basal bulb pyriform, slightly larger than median bulb, offset from intestine. Excretory pore behind nerve ring. Postrectal intestinal sac present. Vulva transverse, lips not raised. **Vagina sclerotized.** Spermathecae round or oval. Ovaries outstretched. **Female tail elongate-filiform** to an attenuated tip, hyaline portion more than half tail length. Phasmids about one anal body width behind anus. Male tail short, conical, enclosed in a trilobed bursa; lateral lobes of bursa large. Spicules apparently not flanged. Gubernaculum robust, trough-shaped.

## Type species

*Brachydorus tenuis* de Guiran & Germani, 1968

## Other species

*Brachydorus kazirangai* Rahaman, Ahmad, Khan & Ahmad, 1992

*Brachydorus swarupi* Koshy, Raski & Sosamma, 1981

ETYMOLOGY. From Greek *brachys* = short, and *dory* = spear.

The type species was collected from soil around roots of *Ravenala madagascariensis* Gmel. (Musaceae), at Mahaso, Ivondro Tamatave valley, Malagasy. It has also been found in South Africa.

**FAMILY BELONOLAIMIDAE****(The sting nematodes)**

This family comprises migratory ectoparasites of roots which are known as sting nematodes. They have long stylets and feed on deeper root tissues. They are generally restricted in geographical distribution, e.g. *Belonolaimus* spp. to North America, *Ibipora* to Central and South America, and *Carphodorus* and *Morulaimus* to Australia and New Zealand.

*Belonolaimus* spp. parasitize grasses in the USA and are important pests of turf in lawns and golf courses. *Belonolaimus longicaudatus* is widely distributed in the Atlantic coastal plains from Virginia to Florida and has been reported from Mexico and Central America. It is pathogenic to grapefruit (Standifer & Perry, 1960) and

attacks maize, cotton, strawberry and several vegetables in Florida, USA. The life cycle takes about 28 days and the optimum temperature for reproduction is 30°C. There is evidence for the occurrence of three physiological races of *B. longicaudatus* in Florida (Abu-Gharbieh & Perry, 1970). *Belonolaimus gracilis* builds up large populations on Gramineae (grasses, barley, maize, oat, rye, wheat) and is an important parasite of several field crops (beans, celery, cotton, cowpea, onion, peanut, squash, strawberry) in southern USA (Holdeman & Graham, 1953).

## Family Belonolaimidae Whitehead, 1960 (Siddiqi, 1970)

### Diagnosis

Dolichodoroidea. Medium to large nematodes ( $L = 1\text{--}3\text{ mm}$ ). Lateral fields each with one, two or four incisures, areolated. Deirids absent. Phasmids on tail. Amphidial apertures obscure, probably longitudinal cleft-like. Cephalic region offset by a constriction, rarely continuous, finely but distinctly annulated (annules six to ten), **usually four-lobed, lateral sectors much smaller than submedians; labial disc prominent**, round to lemon-shaped; six pits around oral aperture; framework sclerotized, its inner margins extend as elongated, **tubular vestibulum extension**, posteriorly giving support for the attachment of most of the protractor myofibrils. **Stylet very long (60–150  $\mu\text{m}$ ), conus 55–80% of its total length**; knobs rounded. **Precorpus with convoluted lumen**. Postcorpus very muscular, oval to rounded. **Isthmus short**. Oesophageal glands extending over intestine latero-dorsally, laterally or latero-ventrally; dorsal gland larger and longer than subventrals. **Oesophago-intestinal junction indistinct; less than one corresponding body width from median bulb**. Intestinal fasciculi present. **Vulva with epiptygma**. Vagina in a few species sclerotized. Ovaries paired, outstretched. Spermathecae axial or slightly offset. Female tail cylindroid, subcylindroid or conoid, over one and a half anal body widths long. **Male tail elongate-conoid; bursa simple, enclosing tail tip**. Testis single, outstretched. Spicules well developed. **Gubernaculum large, modified, usually with titillae and recurved distal end**. Migratory ectoparasites of roots (generally Gramineae), mostly inhabitants of sandy soils.

### Type subfamily

Belonolaiminae Whitehead, 1960

No other subfamily.

## Subfamily Belonolaiminae Whitehead, 1960

### Diagnosis

With the characters of the family Belonolaimidae.

### Type genus

*Belonolaimus* Steiner, 1949

### Other genera

*Carphodorus* Colbran, 1965

*Ibipora* Monteiro & Lordello, 1977

*Morulaimus* Sauer, 1966

### Key to genera of Belonolaiminae

1. Lateral field with single groove-like incisure, originating from cephalic region ..... *Belonolaimus*  
 Lateral field with two to four incisures, originating well behind cephalic region ..... 2
2. Cephalic region distinctly four-lobed ..... *Ibipora*  
 Cephalic region not distinctly four-lobed ..... 3
3. Perioral disc rounded; lateral field with only two inner incisures distinct ..... *Carphodorus*  
 Perioral disc lemon-shaped; lateral field with all four incisures distinct ..... *Morulaimus*

### Genus *Belonolaimus* Steiner, 1949

(Fig. 99, A–E)

#### Diagnosis

Belonolaiminae. Large-sized (2–3 mm), slender ( $a = 50\text{--}80$ ). **Lateral field with a single incisure or groove from head to tail**, indenting annular contour. Phasmids pore-like, inconspicuous, near middle of tail. Cephalic region large, rounded, offset (except in female of *B. euthychilus*), divided by longitudinal grooves into four well-separated sectors – two subdorsals, two subventrals; two very small lateral pseudolips present near apex and bear inconspicuous amphidial apertures; **labial disc offset, rounded, conspicuous**; framework with basal plate moderately and arches lightly sclerotized. Excretory pore near oesophago-intestinal junction. **Stylet very long (90–160  $\mu\text{m}$ )**, with conus more than twice shaft length. Median bulb round, isthmus short, **oesophago-intestinal junction lies close to median bulb**, anterior to main body of glands. **Oesophageal glands overlapping intestine latero-ventrally**. Intestinal fasciculi thick, conspicuous. Vulva equatorial, with epitygma. Spermathecae axial, slightly offset. Ovaries paired. **Tail elongate**, in female cylindroid, three to six anal body widths long; with **postanal extension of intestine, and annulated terminus**; in male elongate-conoid, enveloped by a low bursa. Spicules robust; slightly arcuate, flanged. Gubernaculum large, not protrusible, proximal end directed posteriorly.

#### Type species

*Belonolaimus gracilis* Steiner, 1949

#### Other species

*Belonolaimus euthychilus* Rau, 1963

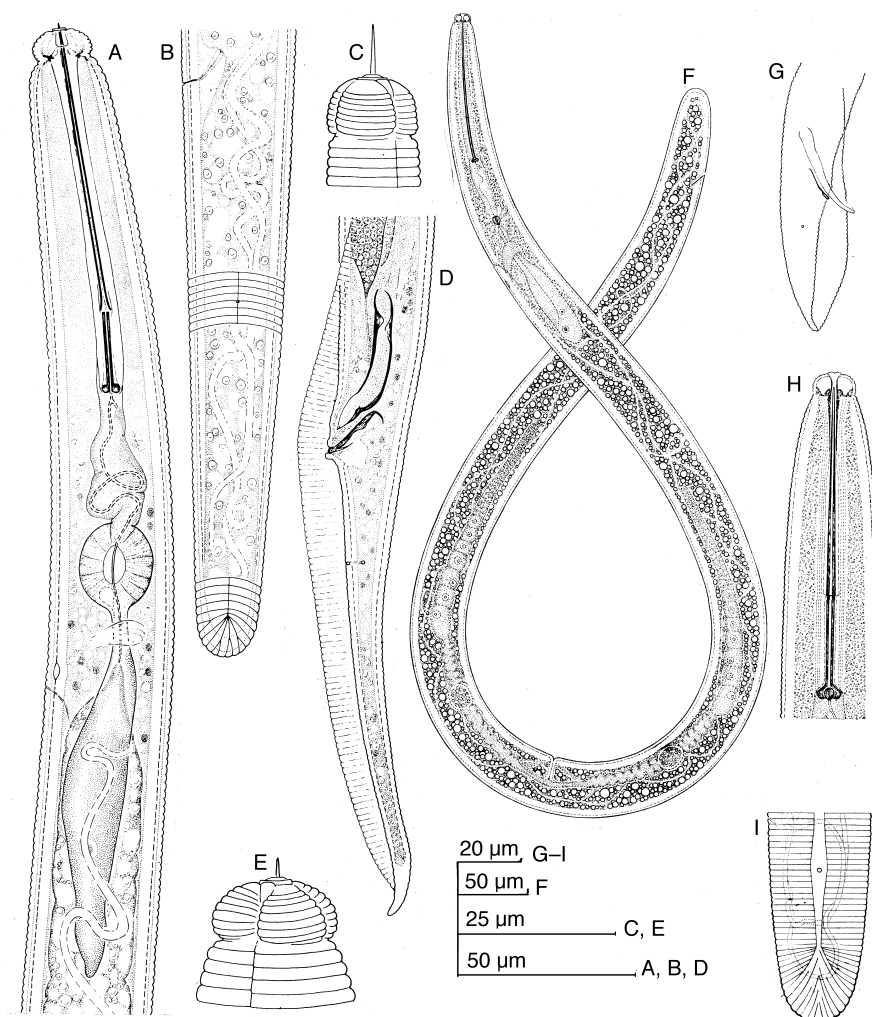
*B. longicaudatus* Rau, 1958

*B. maritimus* Rau, 1963

*B. nortoni* Rau, 1963

ETYMOLOGY. From Greek *beloné* = arrowhead, needle (stylet), and *laimos* = throat.





**Fig. 99.** A–E. *Belonolaimus longicaudatus* Rau. A. Oesophageal region. B. Female tail. C. Male head end. D. Male tail. E. Female head end. F–I. *Carphodorus bilineatus* Colbran. F. Female. G. Male tail. H. Female head end. I. Female tail end (A–E. After Orton Williams (1974): CIH Descriptions of Plant-parasitic Nematodes. F–I. After Colbran (1965a), courtesy Queensland Journal of Agricultural and Animal Sciences.)

The type species was found on maize roots at Sanford, Florida, and also on roots of slash and long leaf pine in Florida, USA. *Belonolaimus* spp. mostly parasitize grasses and other monocotyledonous plants and gymnosperms; some species also attack dicots, especially leguminous plants. They may occur in brackish soils.

**Genus *Carphodorus* Colbran, 1965**

(Fig. 99, F–I)

**Diagnosis**

Belonolaiminae. Medium-sized (about 1 mm). Lateral fields each with four incisures, of which only inner ones are distinct. Phasmids in anterior region of tail. Cephalic region offset by a constriction; not **four-lobed; anteriormost annule divided into six sectors, of which laterals are slightly smaller than the submedians; labial disc rounded, offset**; amphidial apertures between labial disc and lateral sector; framework strongly sclerotized. Stylet very long (90–97  $\mu\text{m}$  in female, 70–83  $\mu\text{m}$  in male in type species), conus about twice as long as shaft. Orifice of dorsal gland about 3–4  $\mu\text{m}$  behind stylet base. Median bulb oval, very muscular. Isthmus short. Oesophageal glands overlapping intestine laterally and latero-dorsally; oesophago-intestinal junction opposite posterior half of glands. Intestine with thin, faint fasciculi; extending into tail. Vulva submedian (at 55–57%). Ovaries paired, outstretched, oocytes in most part in double rows. Spermathecae axial, sub-spherical. **Female tail short, subcylindrical**, about one and a half to two anal body widths long, annulated at tip. Bursa well developed, enveloping tail. Spicules slightly arcuate, 26–33  $\mu\text{m}$  long in type species, with blunt tip. Gubernaculum about half as long as spicule, proximal end directed slightly dorsally, with distal titillae.

**Type species***Carphodorus bilineatus* Colbran, 1965

No other species.

ETYMOLOGY. From Greek *karphe* = a straw, shrunk; and *dory* = spear.

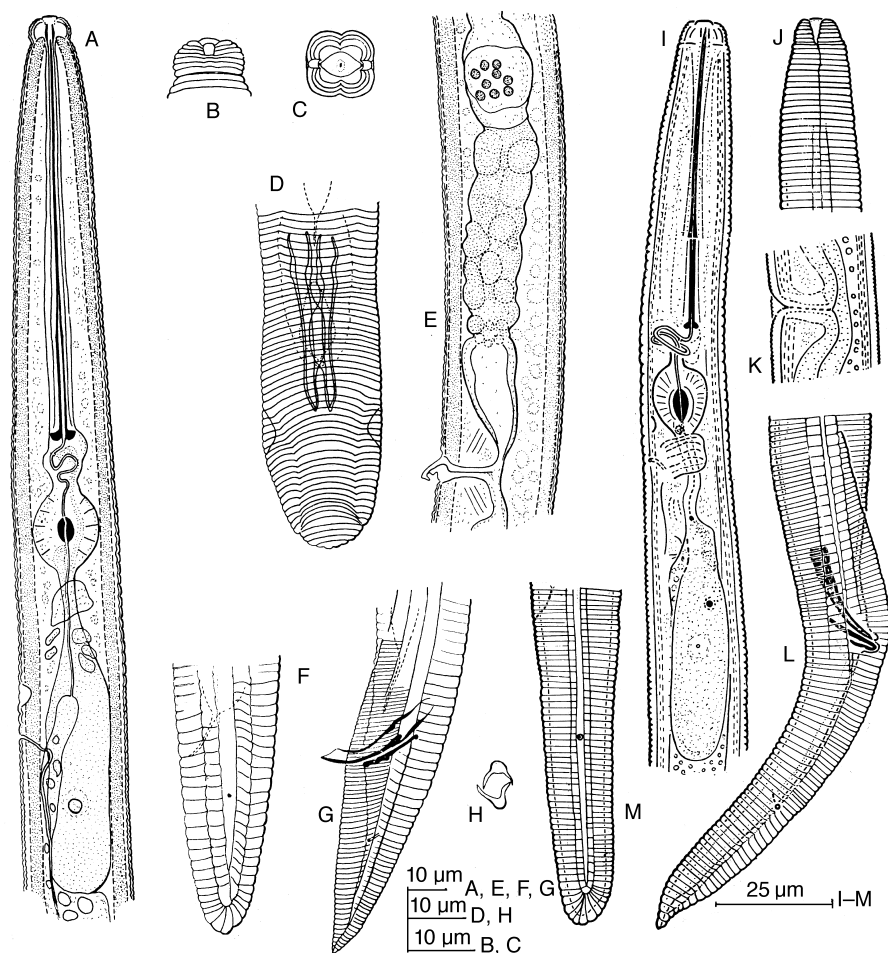
The type species was found in eucalyptus forest around the roots of *Eucalyptus andrewsi* Maiden and *Casuarina littoralis* Salisb. in Queensland, Australia.

**Genus *Morulaimus* Sauer, 1966**

(Fig. 100, A–H)

**Diagnosis**

Belonolaiminae. Medium to large (about 1–2 mm). **Lateral field with four distinct incisures, outer bands areolated**. Phasmids generally in anterior half of tail. Cephalic region offset, usually by a constriction, **in four sectors, not well separated; labial disc indistinct, lemon-shaped**; amphidial apertures between labial disc and reduced lateral pseudolips; basal plate lightly to moderately sclerotized. **Stylet very long** (57–113  $\mu\text{m}$ ), conus 60–75% of total stylet length, knobs flattened anteriorly. Precorpus with convoluted lumen. Median bulb rounded, very muscular. Isthmus short, or long. Excretory pore opposite or behind oesophago-intestinal junction. Oesophageal glands overlapping intestine latero-dorsally; oesophago-intestinal junction opposite anterior half of glands. Intestinal fasciculi faint, thin. **Vulva** median to postmedian (at 51–58%), **with conspicuous epitygma**. Spermathecae axial, slightly offset. Ovaries paired, outstretched. Female tail cylindroid to conical, short, about 1.7–3 anal body widths long; terminus hemispherical to conoid-



**Fig. 100.** A–H. *Morulaimus arenicolus* Sauer. I–M. *Ibipora jara* Monteiro & Lordello. A and I. Female oesophageal regions. B and C. Female heads, lateral and *en face* view, respectively. D, G and L. Male tails. E and K. Vulval regions. F and M. Female tails. H. Spicular flanges, end-on view. J. Anterior end of female. (A–H. After Sauer (1966), courtesy *Nematologica*. I–M. After Monteiro & Lordello (1977), courtesy *Revista de Agricultura, Brazil*.)

rounded, usually annulated. Bursa well developed, enveloping entire tail. Spicules about 30–36  $\mu\text{m}$  long, cephalated, arcuate, flanged. Gubernaculum large, protrusible, about half as long as spicule, with round proximal end which may be slightly directed posteriorly.

#### Type species

*Morulaimus arenicolus* Sauer, 1966

## Other species

- Morulaimus geniculatus* Sauer, 1966  
 syn. *Scutellonema magnum* Yeates, 1967  
*Morulaimus magnus* (Yeates) Siddiqi, 1986  
*M. gigas* Nobbs & Eyres, 1992  
*M. sclerus* Sauer, 1966  
*M. simplex* Sauer & Annells, 1981  
*M. simpsoni* Nobbs, 1990  
*M. soldus* Colbran, 1969  
*M. whitei* (Fisher, 1965) Sauer, 1966  
 syn. *Telotylenchus whitei* Fisher, 1965

ETYMOLOGY. From Latin *morus* = mulberry, and Greek *laimos* = throat.

The type species was found in uncultivated soil, Calder Highway, Hattah, Victoria, Australia. The genus is confined to Australia. A key to *Morulaimus* spp. is given by Nobbs and Eyres (1992).

**Genus *Ibipora* Monteiro & Lordello, 1977**

(Fig. 100, I–M)

## Diagnosis

Belonolaiminae. Medium to large (1–1.8 mm). Cuticle prominently annulated. Lateral fields each with four distinct incisures making three bands, outer bands areolated. Deirids absent. Phasmids pore-like, near middle of tail. Cephalic region offset, in **four large submedian sectors well separated by grooves**, appearing similar to that of *Belonolaimus*; small lateral sectors present; labial disc round, offset. Stylet 62–100  $\mu\text{m}$ , conus more than twice as long as shaft, knobs small, rounded. Median bulb large, spheroidal, with large refractive thickenings. Isthmus slender. Oesophageal glands overlapping intestine laterally; **oesophago-intestinal junction anterior to glands, about a body width or less behind median bulb**. Excretory pore behind hemizonid. Intestine usually extends into tail cavity; fasciculi distinct. Vulva median, in a body cavity or depression, with inconspicuous epitygma and lateral membranes; vaginal sclerotization may be present. Spermathecae axial, slightly offset. Ovaries paired, outstretched. Female tail cylindrical to subcylindrical, with obtusely rounded or conoid terminus. Male tail elongate-subcylindrical to a conical tip, completely enveloped by a simple, moderately developed bursa arising much anterior to heads of spicules. Spicules arcuate. Gubernaculum recurved distally.

## Type species

- Ibipora jara* Monteiro & Lordello, 1977  
 syn. *Belonolaimus jara* (Monteiro & Lordello) Fortuner & Luc, 1987

## Other species

- Ibipora anama* Monteiro & Lordello, 1977  
 syn. *Belonolaimus anama* (Monteiro & Lordello) Fortuner & Luc, 1987  
*I. lineatus* (Román, 1964) Monteiro & Lordello, 1977

syn. *Belonolaimus lineatus* Román, 1964  
*I. lolii* (Siviour, 1978) Siviour & McLeod, 1979  
 syn. *Belonolaimus lolii* Siviour, 1978

ETYMOLOGY. The name *Ibipora* is derived from the Tupi language, meaning 'soil inhabitant', and is not feminine due to its ending -a, but is masculine in gender as stated by its proposers (ICZN Article 30d).

The type species was described from sugarcane soil, Usina Maracai, Assis, State of São Paulo, Brazil. The genus parasitizes roots of sugarcane in Brazil (*I. jara*, *I. anama*) and Puerto Rico (*I. lineatus*) and grasses in Australia (*I. lolii*). A key to species was given by Doucet (1983).

## FAMILY TELOTYLENCHIDAE

### (The stunt nematodes)

The stunt nematodes, e.g. *Tylenchorhynchus*, *Quinisulcius*, *Merlinius* and *Bitylenchus* spp., are root surface tissue feeders, polyphagous in nature and are commonly found in vegetable fields, grasslands and forest soils. *Tylenchorhynchus silvaticus* was found on several occasions in undisturbed forest soil in Illinois, USA. It readily builds up high populations on rye. *Tylenchorhynchus ewingi* and *T. claytoni* cause stunting of root tips, chlorosis and retarded growth, sometimes resulting in death of forest tree seedlings in USA nurseries (Hopper, 1959). *Tylenchorhynchus claytoni* reduces the root systems of barley, maize, cotton, oat, potato, soybean, etc., causing damage to these crops in the USA. It is bisexual and completes its life cycle in about a month. This species and *B. dubius* parasitize a number of grasses, reducing vegetative growth in several States of the USA.

*Tylenchorhynchus mexicanus* was associated with roots of cactus, green beans and tobacco in Mexico where *Quinisulcius* spp. were found on bamboo, grasses and sunflower. *Quinisulcius acti* (= *Q. capitatus*) partially penetrates into the maize roots and causes lesions in epidermal, subepidermal and cortical tissues (Vovlas, 1983). Several species of *Tylenchorhynchus* attack vegetables and fruit trees in India (Siddiqi, 1961b).

On red clover roots, *T. agri* always fed ectoparasitically and singly, usually on epidermal cells with only the stylet tip being inserted into the cells. Feeding duration was usually less than 5 min. The cells fed upon for more than 30 min had granular cytoplasm and increased cyclosis, but 10 h after feeding, these cells appeared normal (Coates-Beckford, 1982). *Bitylenchus dubius* feeds primarily on root hairs and epidermal cells just behind the meristematic regions of grass roots. It suppresses secondary stolon formation and causes shortened internodes and premature inflorescence initiation. It feeds on the epidermal tissue of the young roots of cotton and Tepari beans. *Bitylenchus maximus* and *Neodolichorhynchus lamelliferus* also feed on epidermal root cells but aggregate on root tips.

*Merlinius* spp. generally feed on root hairs or epidermal cells. *Merlinius brevidens* is an ectoparasite that moves rapidly from one feeding site to another, feeding on root hairs and epidermal cells. *Amplimerlinius icarus* and *A. macrurus*, on the other

hand, feed deeper on the cortical cells and remain at one site feeding continuously for many hours or days (Bridge & Hague, 1974).

*Tylenchorhynchus annulatus* (= *T. martini*) is an important parasite of rice and sugarcane in many tropical and subtropical areas. Some nematodes show the phenomenon of swarming. Rice plants growing in soil infested with swarming *T. annulatus* were more severely stunted and chlorotic and had reduced growth than those in soil with non-swarming *T. annulatus*. The swarmers tend to stick to each other and there are differences in morphology, physiology and pathogenicity between nematodes of swarming and non-swarming populations (Ibrahim & Hollis, 1973).

Sher (1974) differentiated *Triversus* from *Tylenchorhynchus* by having three incisures (*sensu Divittus*), by the shape of the lip region, pointed female tail and bursa not enclosing tail tip. Examination of the type species, *Triversus annulatus*, and another undescribed species of *Triversus* shows that the character of the conical female tail with a pointed tip remains the sole difference between *Triversus* and *Tylenchorhynchus* since the bursa may envelop the tail tip and the lateral field may have four incisures. *Tylenchorhynchus paulettae* Bloemers & Wanless, 1998 has head region and tail typical of the genus *Triversus* but the lateral field has four incisures. *Meiodorus*, which was synonymized with *Triversus* by Fortuner & Luc (1987), differs from *Triversus* in having an elongate female tail with a distinct narrow terminal hyaline region, median oesophageal bulb in posterior half of oesophagus, gubernaculum lacking a **crest** (see Gomez-Barcina *et al.*, 1992) and male tail distinctly shorter than that of the female and carrying a trilobed bursa. The bursa in *Meiodorus* is like that of *Dolichodorus*/*Neodolichodorus*/*Brachydorus* and is different in shape and structure from that of *Tylenchorhynchus*/*Mulkorhynchus*/*Triversus*. This type of bursa is not found in Telotylenchinae and hence the contention of Fortuner & Luc (1987) that, since *Dolichorhynchus* (now *Mulkorhynchus*) and *Triversus* show 'A definite trend towards lobed caudal alae in Telotylenchinae, and this character should not be used as sole criterion for the placement of a taxon in Dolichodoridae', is rejected. Ryss (1993) considered *Meiodorus* and *Brachydorus* in Meiodorinae of the family Meiodoridae. Meiodoridae is not recognized here as a family. Thus, *Triversus* is very similar to *Tylenchorhynchus*, differing only in having a pointed female tail tip while the male tail and bursa are not sufficiently different. Continuous head annules and the gubernaculum bearing a crest in this genus are the same as in *Tylenchorhynchus* and the two genera are not sufficiently different from each other. Bloemers & Wanless (1998) had stated that, without the use of SEM, the genus *Triversus* could no longer justifiably be distinguished as a separate genus from *Tylenchorhynchus*. Hence *Triversus* is regarded as a junior synonym of *Tylenchorhynchus*.

Mulk and Jairajpuri (1974) proposed the genus *Dolichorhynchus* for *Tylenchorhynchus phaseoli* Sethi & Swarup, 1968 and a new species, *D. nigericus*, on the basis of longitudinal cuticular ridges and a notched bursa with a trilobed tip. Jairajpuri & Hunt (1984) erected *Neodolichorhynchus* for those species of *Dolichorhynchus* which did not have a notched bursa and lateral vulval flaps and Jairajpuri (1985) proposed *Prodolichorhynchus* for *Dolichorhynchus elegans* Germani & Luc, 1984, on the basis of having a single ridge (two incisures) in the lateral field. Finding that *Dolichorhynchus* was occupied by the name of a Cephalochordata, i.e. *Dolichorhynchus* Willey, 1901, Jairajpuri (1988) proposed a new name, *Mulkorhynchus*, for *Dolichorhynchus* Mulk & Jairajpuri, 1974. *Neodolichorhynchus*, *Mulkorhynchus* and

*Prodolichorhynchus* have longitudinal lamellae or ridges all over the body from head to tail and the head region is indented dorso-ventrally. Dorso-ventral indentation of annules in the lip region is also found in *Bitylenchus*. Baujard *et al.* (1994a) gave SEM illustrations of face views of several species of *Tylenchorhynchus*, *sensu lato*, including those now in *Neodolichorhynchus*, showing heterogeneity in head indentation. Fortuner & Luc (1987) did not recognize the value of lip region indentation but Talavera & Tobar (1997), who reviewed the taxonomy of this group, pointed out that *Trilineellus* has a head region rounded in face view as in *Tylenchorhynchus* and that it is different from *Neodolichorhynchus* which has a dorso-ventrally indented head. They stated that cuticular longitudinal ridges were different from longitudinal lines and were a valid criterion to differentiate genera. The differentiating characters of *Mulkorhynchus* and *Prodolichorhynchus* from *Neodolichorhynchus* (number and height of ridges, complete vs. incomplete areolation of the lateral fields, and presence of lateral vulval membranes and of notches at the bursa tip) are considered of subgeneric value and therefore *Mulkorhynchus* and *Prodolichorhynchus* are proposed as subgenera of *Neodolichorhynchus* (see Mulk & Siddiqi, 1982; Talavera & Tobar, 1997).

*Trilineellus* has a tessellated cuticle and cephalic region with a few annules which are smooth and un-indented laterally and hence cannot be differentiated from *Tylenchorhynchus* (cf. *Tessellus* and *Divittus*) and has rightly been synonymized with it by Fortuner & Luc (1987).

*Divittus* and *Morasinema* were published on the same date by Jairajpuri (1984) and Javed (1984), based on the same type species, i.e. *Tylenchorhynchus divittatus* Siddiqi, and were differentiated from *Tylenchorhynchus* only by the presence of three incisures as against four in the latter. Later, Jairajpuri (1984a), as the first reviser, proposed *Morasinema* as a junior synonym of *Divittus* (also see remarks under *Neodolichodorus*). *Divittus* (= *Morasinema*) is at present regarded as a junior synonym of *Tylenchorhynchus* until more characters are found to differentiate them. Similarly, *Tessellus* Jairajpuri & Hunt, which is differentiated from *Tylenchorhynchus* only by the tessellated cuticle, is not recognized.

The subfamily Dolichorhynchinae was proposed for longitudinal lamellae-bearing nematodes, which otherwise are typically Telotylenchinae. These lamellae are higher when fewer in number than when numerous; and in the latter case, the cuticular pattern is hardly distinguishable from that of the forms having a tessellated cuticular surface caused by the longitudinal and transverse striations (e.g. *Tylenchorhynchus claytoni*, *T. pachys*). On this sole cuticular character, Dolichorhynchinae cannot be recognized.

Siddiqi (1976) proposed *Meiodorus* and Meiodorinae for *Meiodorus hollisi* Siddiqi, 1976, collected from rice fields of Louisiana, USA. This nematode has an elongate tapering tail with a conspicuous hyaline terminal portion in the female and a trilobed bursa in the male – characters of the subfamily Dolichodorinae. However, its anterior region is typical of the subfamily Telotylenchinae. Meiodorinae thus occupies an intermediate position between Dolichodorinae and Telotylenchinae. The genus *Mulveyotus* Anderson & Ebsary is based on female characters since a male was not found. It cannot be differentiated from *Meiodorus* and is regarded as a junior synonym of the latter.

The elongation of the stylet in Telotylenchidae occurred independently in

Dolichodorinae, Macrotrophurinae, Telotylenchinae (*Sauertylenchus*) and Merliniinae (*Geocenamus*). Stylets with a solid-appearing tip as found in *Tylenchorhynchus*, *Merlinius*, *Trophurus*, seldom reach a length over 30  $\mu\text{m}$ ; those with a tubular conus have a greater chance of exceeding this length. Stylet length can be used as a generic character with care, but it cannot be the sole basis for grouping genera, e.g. *Dolichodorus*, *Belonolaimus* and *Macrotrophurus*, into one subfamily.

The amphidial apertures are pore-like or dorso-ventrally oval, and are labial in various genera of Telotylenchinae. In *Macrotrophurus* of the Macrotrophurinae they are in the form of dorso-ventral slits and are postlabial. On this character, the genus is closer to the members of the Psilenchidae.

There is a tendency among some nematologists to recognize Tylenchorhynchidae as a family separate from the Dolichodoridae and Belonolaimidae (Golden, 1971; Fotedar & Handoo, 1978). However, in 1960 Siddiqi proposed Telotylenchinae with *Telotylenchus* Siddiqi as its type genus. Telotylenchinae was proposed as a junior synonym of Belonolaiminae by Jairajpuri (1963), but Sauer (1966) rejected that proposal. Siddiqi (1970) raised Belonolaiminae to family rank and assigned Telotylenchinae to it. The close relationship of *Telotylenchus* with *Tylenchorhynchus* was pointed out by Siddiqi (1960). Although *Telotylenchus* differs from *Tylenchorhynchus* only in having the dorsal oesophageal gland extending over the intestine and in having a different face view and structure of the gubernaculum, yet, in the past, the two genera have been considered to belong to separate families (Siddiqi, 1970, 1971; Fotedar & Handoo, 1978). The two genera belong to the same subfamily, Telotylenchinae.

Khan (1986) recognized Tylenchorhynchinae, Merliniinae and Trophurinae under Tylenchorhynchidae of the superfamily Tylenchoidea, and Dolichodorinae, Belonolaiminae, Meiodorinae and Telotylenchinae under Dolichodoridae of the Hoplolaimoidea. Ryss (1993) classified Tylenchorhynchinae, Telotylenchinae, Trophurinae and Macrotrophurinae under Tylenchorhynchidae and elevated Merliniinae and Meiodorinae to family rank. A comparison of the accessory genital structures, e.g. hypopygium and spicule (see Fig. 108(b), E & F), shows that the Merliniinae is a very distinct group from the Telotylenchinae. Merliniidae and Meiodoridae are not recognized at the family level here. Tylenchorhynchinae and Trophurinae are here synonymized with Telotylenchinae, which is the senior family group name.

Siddiqi (1986) assigned *Meiodorus* of Meiodorinae to the family Dolichodoridae. The amphidial apertures of *Meiodorus* are probably pore-like facing anteriorly and the structure of the anterior region, including the stylet, is similar to that of the members of the Telotylenchinae. Unlike the members of the Dolichodoridae, the head is not four-lobed and the basal plate of the labial framework and vaginal walls are not sclerotized. Hence Meiodorinae is here assigned to Telotylenchidae rather than Dolichodoridae.



**Family Telotylenchidae Siddiqi, 1960****syn. Tylenchorhynchidae Eliava, 1964****Merliniidae Siddiqi, 1971 (Ryss, 1993)****Meiodoridae Siddiqi, 1976 (Ryss, 1993)****Diagnosis**

Dolichodoroidea. Small to medium sized (0.5–1.1 mm). Cuticle prominently annulated; longitudinal striae and grooves may be present. **Lateral fields each with three to six incisures. Deirids absent** except in Merliniinae. Amphidial apertures pore-like, labial, at lateral margins of labial disc. Cephalic region annulated; **labial disc indistinct and not marked off from cephalic annules** (except *Sauertylechus*), in SEM, flat squarish or cross-shaped bearing a central oval oral opening surrounded by six labial sensilla; framework with light to moderate sclerotization. **Stylet under 45 µm long**, conus about as long as shaft except *Macrotrophurus* in which stylet is over 80 µm long. Oesophageal glands enclosed in a basal bulb or extending over intestine laterally or latero-dorsally, in latter case dorsal gland enlarged and extending past the subventrals. Vulva transverse. **Vagina not sclerotized**. Ovaries paired. Female tail generally two to four anal body widths long, terminus variable. Male tail elongate-conoid, enveloped by a **simple bursa** or trilobed in Meiodorinae. Spicules arcuate with large distal flanges (vela), **tip narrowly pointed or indented**. Gubernaculum rod-like, protrusible or fixed. Ectoparasites of roots.

**Type subfamily**

Telotylenchinae Siddiqi, 1960

**Other subfamilies**

Macrotrophurinae Fotedar &amp; Handoo, 1978

Meiodorinae Siddiqi, 1976

Merliniinae Siddiqi, 1971

**Key to subfamilies of Telotylenchidae**

1. Deirids present (except in *Scutylechus*), lateral field with six incisures; male with hypopygma; spicules cylindrical, not flanged ..... **Merliniinae**  
 Deirids absent, lateral field with two to five incisures; male without hypopygma; spicules flanged ..... **2**
2. Amphidial apertures conspicuous, postlabial; stylet over 80 µm long ..... **Macrotrophurinae**  
 Amphidial apertures inconspicuous, labial; stylet under 50 µm long ..... **3**
3. Male tail conspicuously shorter than that of female; bursa trilobed ..... **Meiodorinae**  
 Male tail not conspicuously shorter than that of female; bursa simple ..... **Telotylenchinae**

**Subfamily Telotylenchinae Siddiqi, 1960**  
**syn. Tylenchorhynchinae Eliava, 1964**  
**Trophurinae Paramonov, 1967**  
**Dolichorhynchinae Fotedar & Handoo, 1978**

**Diagnosis**

Telotylenchidae. Cuticle prominently annulated; longitudinal striae and grooves may be present, not distinctly two-layered. Lateral fields each with three to five incisures. Amphidial apertures pore-like, labial, indistinct. **Deirids absent**. Cephalic region annulated; rounded in cross-section; labial disc indistinct (except *Sauertylenchus*), in SEM squarish or cross-shaped. Cephalic sclerotization light to moderate. **Stylet small to moderately long (about 11–40  $\mu\text{m}$ ), with conus about as long as shaft** and distinct basal knobs. Median oesophageal bulb well developed; oesophageal glands enclosed in a basal bulb or dorsal gland enlarged, forming a long lobe extending over intestine. Vulva slit-like, lacking epiptygma. Vagina not sclerotized. Ovaries paired except in *Trophurus*. Spermathecae round, axial. Postrectal intestinal sac generally absent, present in *Bitylenchus* and *Histotylenchus*. Female tail conoid, subcylindroid, cylindroid or subclavate, rarely spicate, between two and six anal body widths long; terminal cuticle may occasionally be strongly thickened as in *Trophurus* and *Paratrophurus*. Male tail conical, about as long as that of female. Bursa simple, well developed, enveloping tail; its tip may be doubly indented (*Neodolichorhynchus*). **Hypoptygma** (a pair of papillae on posterior lip of cloaca) **absent**. Spicules arcuate, with large distal flanges and pointed or indented tip. Gubernaculum rod-like, usually protrusible, distally boat-shaped in lateral view, with or without a crest.

**Type genus**

*Telotylenchus* Siddiqi, 1960

**Other genera**

*Bitylenchus* Filipjev, 1934

*Histotylenchus* Siddiqi, 1971

*Neodolichorhynchus* Jairajpuri & Hunt, 1984

Subgenera: *Neodolichorhynchus* Jairajpuri & Hunt, 1984

*Mulkorhynchus* Jairajpuri, 1988

*Prodolichorhynchus* Jairajpuri, 1985

*Paratrophurus* Arias, 1970

*Quinisulcius* Siddiqi, 1971

*Sauertylenchus* Sher, 1974

*Telotylenchoides* Siddiqi, 1971

*Trichotylenchus* Whitehead, 1960

*Trophurus* Loof, 1956

*Tylenchorhynchus* Cobb, 1913

*Uliginotylenchus* Siddiqi, 1971

**Key to genera of Telotylenchinae**

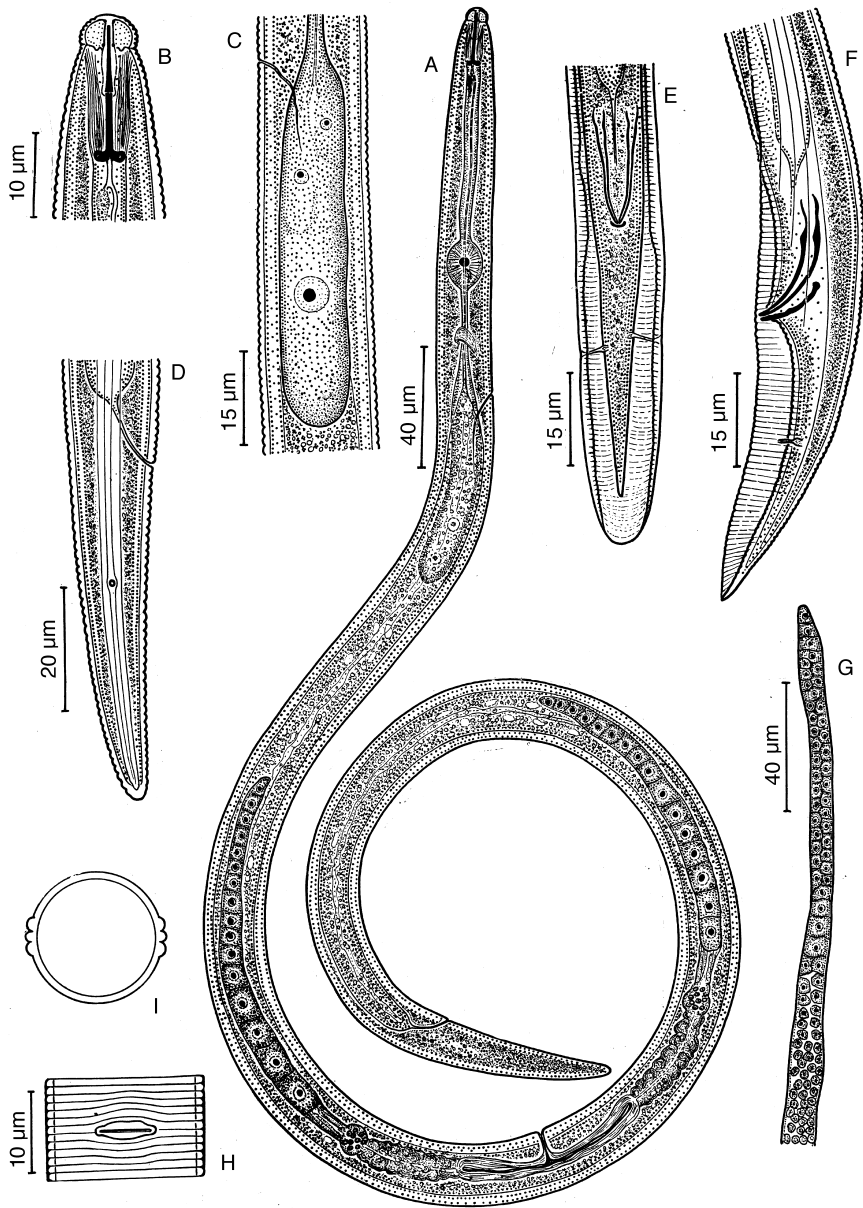
1. Oesophageal glands extending over intestine ..... 2  
    Oesophageal glands not extending over intestine ..... 5
2. Conus of stylet asymmetrical, with lumen becoming angular near its base;  
    intestine extending over rectum into tail ..... *Histotylenchus*  
    Conus of stylet symmetrical, with straight lumen; intestine not extending over  
    rectum into tail ..... 3
3. Cephalic region narrow, conoid-rounded; tail with abnormally thickened  
    cuticle at terminus ..... *Telotylenchoides*  
    Cephalic region broadly rounded; tail without thickened cuticle ..... 4
4. Lateral field with three incisures; stylet extremely attenuated; proximal end  
    of gubernaculum directed posteriorly ..... *Trichotylenchus*  
    Lateral field with four incisures; stylet not attenuated; proximal end of  
    gubernaculum not directed posteriorly ..... *Telotylenchus*
5. Posterior branch of female reproductive system reduced to a sac ..... *Trophurus*  
    Posterior branch of female reproductive system normal ..... 6
6. Cuticle with prominent longitudinal ridges outside lateral fields  
    ..... *Neodolichorhynchus*  
    Cuticle without prominent longitudinal ridges outside lateral fields ..... 7
7. Lateral field with five incisures ..... *Quinisulcius*  
    Lateral field with three or four incisures ..... 8
8. Lateral field with three incisures, areolated; vulva in a body depression, with  
    small epiptygma; proximal end of gubernaculum posteriorly directed  
    ..... *Uliginotylenchus*  
    Lateral field with three or four incisures, if three then not areolated; vulva  
    generally not in a body depression, without epiptygma; proximal end of  
    gubernaculum not posteriorly directed ..... 9
9. Cephalic region annules indented laterally; outer bands of lateral field  
    areolated, gubernaculum lacking a crest ..... 10  
    Cephalic region annules not indented laterally; outer bands of lateral field  
    generally not areolated, gubernaculum having a crest ..... 11
10. Labial disc conspicuous; stylet over 30  $\mu\text{m}$  long ..... *Sauertylenchus*  
    Labial disc not conspicuous; stylet under 30  $\mu\text{m}$  long ..... *Bitylenchus*
11. Tail terminal cuticle abnormally thickened ..... *Paratrophurus*  
    Tail terminal cuticle not abnormally thickened ..... *Tylenchorhynchus*

**Genus *Telotylenchus* Siddiqi, 1960**

(Figs 101; 104(b)C)

**Diagnosis**

Telotylenchinae. Small to medium-sized (0.5–1.1 mm), arcuate upon relaxation. Lateral fields plain or areolated. Cephalic region hemispherical to broadly rounded,



**Fig. 101.** *Telotylenchus indicus* Siddiqi. A. Female. B and D. Head and tail ends of female. C. Oesophageal glands. E and F. Ventral and lateral views of male tail. G. Testis. H. Vulva in ventral view. I. Cross-section of body showing lateral field ridges. (After Siddiqi (1960), courtesy *Nematologica*.)

offset, with five to eight distinct annules, **in SEM labial annules broken near amphidial apertures**. Stylet moderately developed; **conus solid-appearing anteriorly, straight**; knobs prominent. **Dorsal oesophageal gland elongate**, extending over intestine mostly laterally. Vulva flush with body contour or rarely in a small body cavity, epitygma usually absent. Spermathecae round, axial. Ovaries outstretched. **Intestine not extending into tail; fasciculi inconspicuous**. Female tail elongate-conical to subcylindrical, two to four anal body widths long; terminus small; cuticle not abnormally thickened. Bursa large, crenate, **arising well anterior to heads of spicules** and completely enveloping tail, **pre- and postanal stretches of bursa almost equal**. Spicules flanged distally, 21–28  $\mu\text{m}$  long. Gubernaculum large, modified, protrusible; proximal end rounded, not directed posteriorly.

### Type species

*Telotylenchus indicus* Siddiqi, 1960

syn. *Trichotylenchus indicus* (Siddiqi) Jairajpuri, 1971

*Tylenchorhynchus indicus* (Siddiqi) Fortuner & Luc, 1987

### Other species

*Telotylenchus aerolatus* Baqri & Jairajpuri, 1969

syn. *Trichotylenchus aerolatus* (Baqri & Jairajpuri) Jairajpuri, 1971

*Telotylenchus areolatus* Fortuner, 1985 (= junior objective synonym, an unjustified emendation of spelling of *aerolatus*)

*Tylenchorhynchus aerolatus* (Baqri & Jairajpuri) Fortuner & Luc, 1987

*T. avaricus* Kleynhans, 1975

syn. *Tylenchorhynchus avaricus* (Kleynhans) Fortuner & Luc, 1987

*T. crenatus* Kakar, Khan, Siddiqi, 1995

*T. dewaelei* (Kleynhans, 1992) comb. n.

syn. *Tylenchorhynchus dewaelei* Kleynhans, 1992

*T. elongatus* Sultan, Singh & Sakhuja, 1989

syn. *Tylenchorhynchus elongatus* (Sultan, Singh and Sakhuja) Ebsary, 1991

*T. flaccidus* Baydulova, 1984

syn. *Tylenchorhynchus flaccidus* (Baydulova) Fortuner & Luc, 1987

*T. hastulatus* (Colbran, 1960) Jairajpuri, 1963

syn. *Belonolaimus hastulatus* Colbran, 1960

*Telotylenchus hastulatus* (Colbran) Siddiqi, 1963

*Telotylenchus hastulatus* (Colbran) Fisher, 1965

*Morulaimus hastulatus* (Colbran) Sauer, 1966

*Tylenchorhynchus hastulatus* (Colbran) Fortuner & Luc, 1987

*T. impar* Khan & Darekar, 1979

syn. *Tylenchorhynchus impar* (Khan & Darekar) Fortuner & Luc, 1987

*T. lanceatus* Budurova, 1988

syn. *Tylenchorhynchus lanceatus* (Budurova) Ebsary, 1991

*T. marudharensis* (Lal, Mathur & Rajan, 1990) comb. n.

syn. *Tylenchorhynchus marudharensis* Lal, Mathur & Rajan, 1990

*T. namibiensis* (Rashid & Heyns, 1990) comb. n.

syn. *Tylenchorhynchus namibiensis* Rashid & Heyns, 1990

*T. obtusus* Siddiqi, 1978

- syn. *Tylenchorhynchus obtusus* (Siddiqi) Fortuner & Luc, 1987  
*T. paaloofi* Tikyani & Khera, 1970  
 syn. *Trichotylenchus paaloofi* (Tikyani & Khera) Jairajpuri, 1971  
*Tylenchorhynchus paaloofi* (Tikyani & Khera) Fortuner & Luc, 1987  
*T. tonkiensis* Mulk & Jairajpuri, 1975  
 syn. *Tylenchorhynchus tonkiensis* (Mulk & Jairajpuri) Fortuner & Luc, 1987  
*T. ventralis* Loof, 1963  
 syn. *Trichotylenchus ventralis* (Loof) Jairajpuri, 1971  
*Tylenchorhynchus ventralis* (Loof) Fortuner & Luc, 1987  
*T. verutus* Kleynhans, 1975  
 syn. *Tylenchorhynchus verutus* (Kleynhans) Fortuner & Luc, 1987

## Note

*Telotylenchus aerolatus* and *T. tonkiensis* may be junior synonyms of *T. indicus* and *T. paaloofi*, respectively (Siddiqi, 1978a). *Telotylenchus teres* Khan & Darekar, 1979 has a basal oesophageal bulb with the dorsal gland forming a short lobe and having its nucleus anterior to the oesophago-intestinal junction. Hence it belongs to the genus *Tylenchorhynchus*.

ETYMOLOGY. From Greek *telos* = end, and *Tylenchus*.

The type species was found around grass roots (*Cynodon dactylon*) at Aligarh, Uttar Pradesh, India. Other species were described from Australia, Netherlands, India, Malawi, South Africa and Russia.

## Genus *Histotylenchus* Siddiqi, 1971

(Figs 8(d)A; 102, A–J)

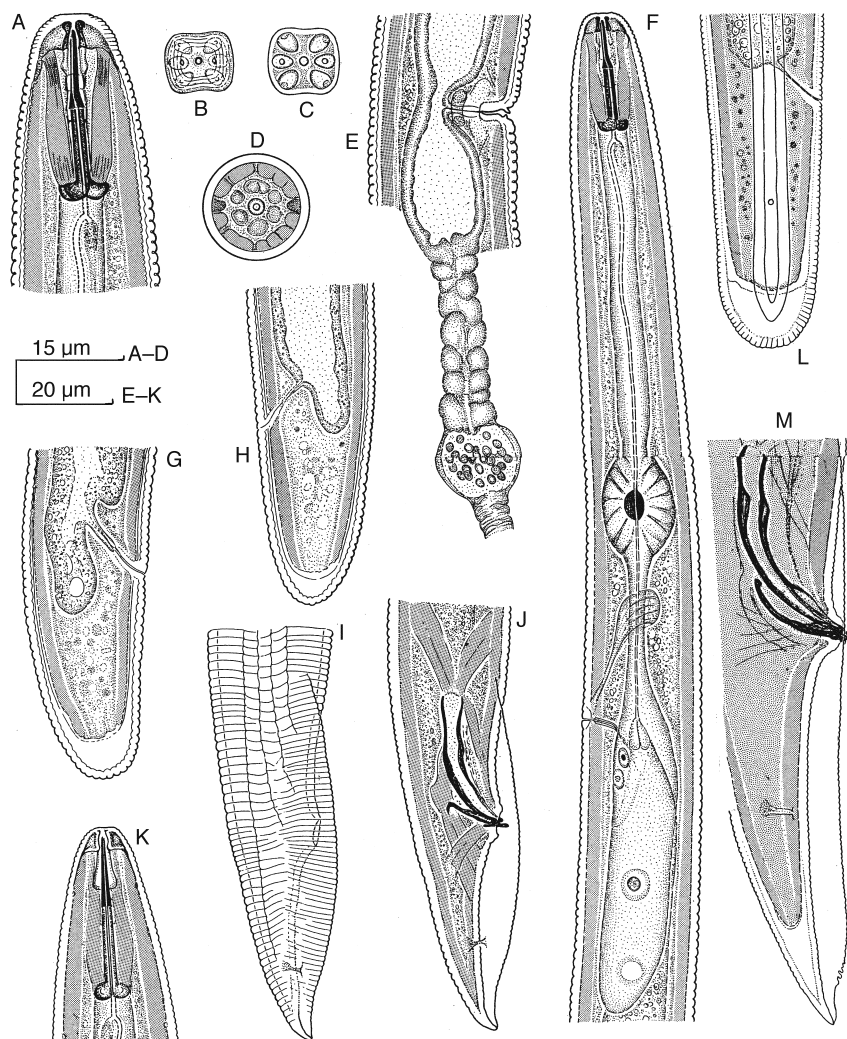
## Diagnosis

Telotylenchinae. Medium-sized (1–1.5 mm), arcuate to strongly curved upon relaxation. **Lateral fields usually areolated.** Deirids indistinct or absent. Phasmids near middle of tail. Cephalic region continuous or slightly offset by a depression, with five to eight distinct annules which are not broken (cf. *Telotylenchus*). Stylet stout, 21–26  $\mu\text{m}$  long; **conus characteristically asymmetrical, with lumen angular near base;** knobs large, with flat to concave anterior surfaces. Median bulb large, oval, with large refractive thickenings. Isthmus short, about half as long as precorpus. **Oesophageal glands extending over intestine;** dorsal gland one and a half to two body widths long, with conspicuous nucleus. Vulva in a cavity, with epiptygma. Ovaries outstretched. Spermathecae axial. **Intestine extending over rectum into tail, with fasciculi.** **Female tail short,** about one and a half to two and a half anal body widths, **cylindrical, subcylindrical to obtuse, with annulated terminus.** Male tail with moderately large bursa arising a little anterior to heads of spicules and enclosing tail tip. Spicules distally flanged. Gubernaculum large (12–15  $\mu\text{m}$ ), with modified proximal end characteristically directed dorsally and backwardly, apparently not protrusible.

## Type species

*Histotylenchus histoides* Siddiqi, 1971

syn. *Paratrophurus histoides* (Siddiqi) Fortuner & Luc, 1987



**Fig. 102.** A–J. *Histotylenchus histoides* Siddiqi. K–M. *Telotylenchoides housei* (Raski, Prasad & Swarup). A and K. Head ends of female. B. *En face* view. C. Cross-section through basal plate. D. Cross-section of body near middle of stylet. E. Vulval region. F. Oesophageal region of female. G, H and L. Tail ends of female. I, J and M. Tail ends of male. (A–M. After Siddiqi (1971a), courtesy *Nematologica*.)

### Other species

*Histotylenchus baoulensis* (Netscher & Germani, 1969) Siddiqi, 1971

syn. *Telotylenchus baoulensis* Netscher & Germani, 1969

*Trichotylenchus baoulensis* (Netscher & Germani) Jairajpuri, 1971

*Paratrophurus baoulensis* (Netscher & Germani) Fortuner & Luc, 1987

*H. hedys* Kleynhans, 1975

syn. *Paratrophurus hedys* (Kleynhans) Fortuner & Luc, 1987

- H. historicus* (Jairajpuri & Baqri, 1968) Siddiqi, 1971  
 syn. *Telotylenchus historicus* Jairajpuri & Baqri, 1968  
*Trichotylenchus historicus* (Jairajpuri & Baqri) Jairajpuri, 1971  
*Paratrophurus historicus* (Jairajpuri & Baqri) Fortuner & Luc, 1987  
*H. mohalei* Kleynhans, 1992  
*H. sudanensis* Siddiqi, 1978  
 syn. *Paratrophurus sudanensis* (Siddiqi) Fortuner & Luc, 1987, nec *Paratrophurus sudanensis* Decker, Yassin & El Amin, 1975  
*Paratrophurus siddiqii* Fortuner & Luc, 1987 (objective syn.)

## Note

Fortuner & Luc (1987) synonymized *Histotylenchus* and *Telotylenchoides* with *Paratrophurus*, but this synonymy was rejected by Castillo *et al.* (1989). These three genera have protoplasmic content of tail regressed, but this character should not be the reason to unite them. *Paratrophurus* is very similar to *Tylenchorhynchus* even in face view and may be its junior synonym. The report of the presence of deirids in *Paratrophurus* by Fortuner & Luc (1987) is an error because deirids are found in Merliniinae, not in Tylenchorhynchinae.

ETYMOLOGY. Greek *histo* = tissue, cellular (for areolated lateral field), *tylos* = knob, and *enchos* = spear.

The type species was found around roots of Napier grass in Malawi.

## Genus *Telotylenchoides* Siddiqi, 1971

(Fig. 102, K–M)

## Diagnosis

Telotylenchinae. Small to medium-sized (about 1 mm or less). Lateral fields not areolated. Phasmids near middle of tail. **Cephalic region small, conoid-rounded, continuous, smooth** or indistinctly annulated, not lobed; **annules broken near amphidial apertures as seen in SEM**; labial disc inconspicuous; **framework strongly sclerotized**. Stylet well developed, 20–23 µm long, **conus tubular with straight lumen**, knobs large. Oesophageal glands extending over intestine laterally and latero-dorsally. Spermathecae axial. Ovaries outstretched. Vulva flush with body, lips not modified, epiptygma absent or indistinct. Female tail cylindrical, with broadly rounded to bulboid terminus; **cuticle at tail tip abnormally thickened**. Bursa well developed, arising a little anterior to head of spicules and completely enveloping tail. Spicules distally flanged, proximal end rounded. Gubernaculum large, modified, proximal end rounded, protrusible.

## Type species

- Telotylenchoides housei* (Raski, Prasad & Swarup, 1964) Siddiqi, 1971  
 syn. *Telotylenchus housei* Raski, Prasad & Swarup, 1964  
*Trichotylenchus housei* (Raski *et al.*) Jairajpuri, 1971  
*Paratrophurus housei* (Raski *et al.*) Andrassy, 1973  
*Paratrophurus housei* (Raski *et al.*) Fortuner & Luc, 1987



### Other species

*Telotylenchoides lobatus* (Loof & Yassin, 1971) Siddiqi, 1971  
syn. *Paratylenchus lobatus* Loof & Yassin, 1971

### Note

The *en face* view in SEM of *Telotylenchoides* shows broken margins of annules near amphidial apertures, the condition similar to that of *Telotylenchus* but different from that of *Tylenchorhynchus* (cf. face views in Sher & Bell, 1975). The head of the type species, *T. housei*, is similar in appearance to that of *Helicotylenchus* as seen under the light microscope and the oesophageal glands form a long lobe over the intestine.

ETYMOLOGY. From *Telotylenchus*, and Greek *eidos* = shape, like.

The type species was found around the roots of *Sorghum vulgare* and *Zea mays* in southern India; *T. lobatus* was collected from soils of *Citrus* spp. and *Ipomoea batatas* in Sudan.

### Genus *Trichotylenchus* Whitehead, 1960

(Figs 103, A–I; 104(b), F)

### Diagnosis

Telotylenchinae. Small to medium-sized (0.6–1 mm), with finely annulated cuticle. **Lateral fields each with three incisures**, usually areolated. Cephalic region continuous, rounded, annulated (three to eight annules), not lobed; labial disc indistinct, **in SEM appears laterally elongated and enclosing amphidial apertures**; framework lightly sclerotized. **Stylet extremely attenuated and slender**, 20–28  $\mu\text{m}$  long; conus solid-appearing for most of its length; **knobs minute**, well separated from shaft. Median bulb oval, very muscular. Oesophageal glands overlapping intestine mostly laterally. Vulva flush with body contour, with inconspicuous epitygma. Spermathecae round or oval, lobed, offset. Ovaries outstretched. **Female tail elongate-cylindroid to subclavate**, 2.6–6 anal body widths long, terminus broadly rounded, annulated. Bursa moderately developed, completely enveloping tail. Spicules flanged. Gubernaculum modified, **proximal end directed dorsally and posteriorly**.

### Type species

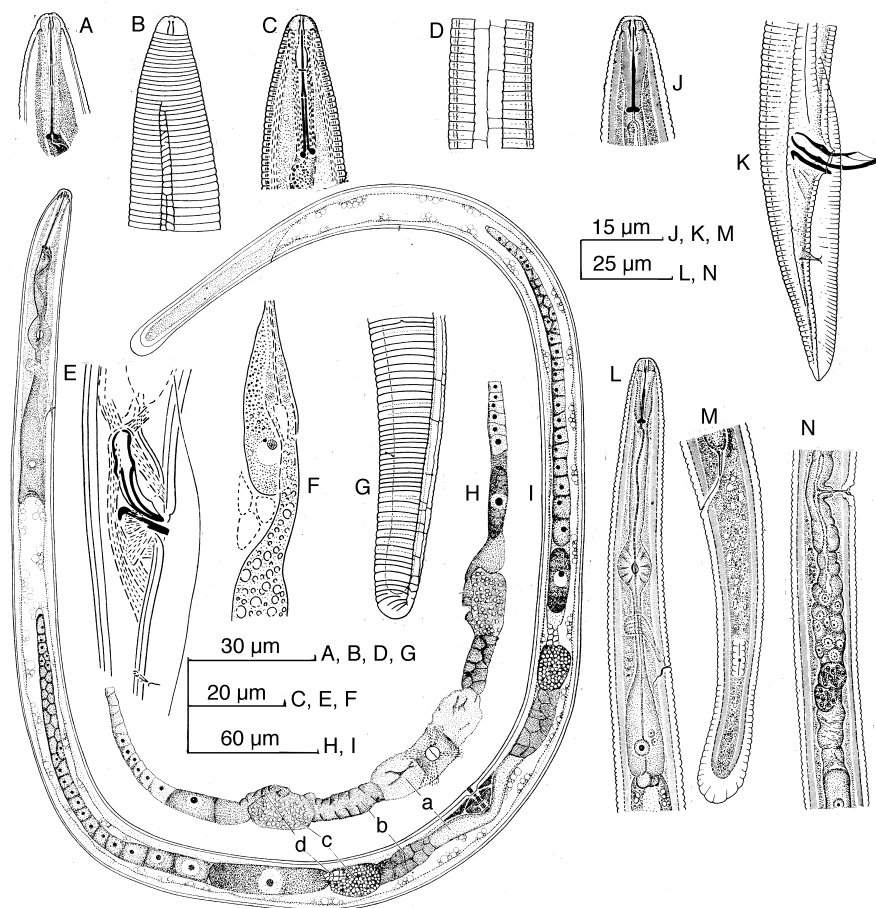
*Trichotylenchus falciformis* Whitehead, 1960

### Other species

*Trichotylenchus astriatoides* Rahman, Ahmad, Khan & Ahmad, 1992  
*T. monosexualis* Kanwar, Bajaj & Dabur, 1993  
*T. rectangularis* Netscher & Germani, 1969

### Note

Several juveniles and a male of *T. falciformis* were found encapsulated in a brownish-yellow cyst-like cocoon in a semi-desiccated rice field – an adaptation to anabiotic conditions.



**Fig. 103.** A–I. *Trichotylenchus falciformis* Whitehead. J–N. *Uliginotylenchus uliginosus* (Siddiqi). A, B and J. Head ends of female. C. Head end of male. D. Lateral field. E and K. Spicular regions. F. Oesophago-intestinal junction. G and M. Tail ends of female. H and N. Female gonads. I. Female. L. Oesophageal region. a, muscular part of the uterus; b, columellar part of the uterus; c, spermatheca; d, proximal part of the oviduct. (A–I. After Coomans and De Grisse (1963), courtesy *Nematologica*.)

**ETYMOLOGY.** Greek *thrix* = hair, *tylos* = knob, and *enchos* = spear (hair-like knobbed spear).

*Trichotylenchus* spp. parasitize monocotyledonous plants (grasses and rice) in Congo, Côte d'Ivoire and Tanzania. The type species was found around roots of grass (*Hyparrhenia* sp.) at 40 miles on the Songea to Tundursu Road, Tanzania.

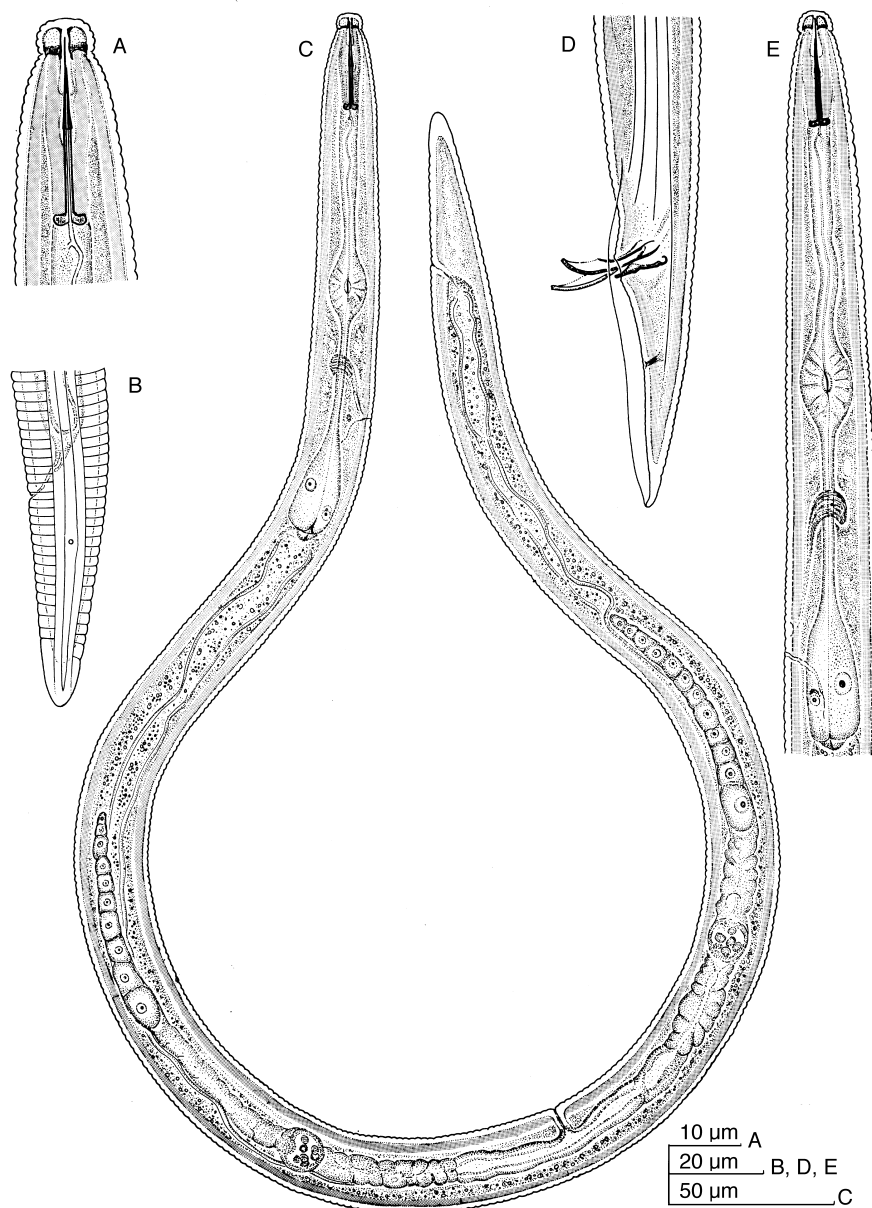
**Genus *Tylenchorhynchus* Cobb, 1913**syn. *Triversus* Sher, 1974*Trilineellus* Lewis & Golden, 1981*Divittus* Jairajpuri, 1984*Morasinema* Javed, 1984*Tessellus* Jairajpuri & Hunt, 1984*Macrorhynchus* Sultan, Singh & Sakhuja, 1991

(Fig. 104(a))

**Diagnosis**

Telotylenchinae. About 1 mm or less long. Cuticle prominently annulated, may be marked by longitudinal striae, **longitudinal ridges or lamellae outside lateral fields absent; not abnormally thickened on tail**. Lateral field with three or four incisures, generally not areolated behind oesophageal region. Cephalic region offset from body (type genus) or continuous, annulated, or rarely smooth, **without longitudinal indentations on annules**; labial disc indistinct, in SEM *en face* squarish, flattened, fused with first lip annule; framework light to moderately sclerotized. Stylet well developed, generally 15–25  $\mu\text{m}$  long; conus anteriorly solid-appearing; knobs prominent. Median bulb round or oval, with distinct refractive thickenings, usually marked off from pre-corpus and isthmus. Basal bulb offset from intestine, or with base slightly extending over intestine. Cardia prominent. Vulva near middle of body, generally at 50–54%, lips not modified. Spermathecae round, axial. Ovaries paired, outstretched. Female tail usually conoid with blunt tip as in type species, but may be subcylindroid, cylindroid or subclavate; terminus smooth, rarely striated or narrowing to a point. Males generally present. Tail enveloped by a large simple bursa. Spicules distally flanged, terminus narrow, indented or pointed. Gubernaculum well developed, about half as long as spicule, generally rod-like and with a velum, **protrusible**.

**Type species***Tylenchorhynchus cylindricus* Cobb, 1913syn. *Tylenchus* (*Tylenchorhynchus*) *cylindricus* (Cobb) Filipjev, 1934*Anguillulina cylindrica* (Cobb) Thorne, 1935**Other species***Tylenchorhynchus aduncus* de Guiran, 1967syn. *Tetylenchus aduncus* (de Guiran) Tarjan, 1973*T. aerolatus* Tobar Jiménez, 1970*T. agri* Ferris, 1963*T. alami* Shaw & Khan, 1996*T. amgi* Kumar, 1981*T. ancorastyletus* Ivanova, 1983 (syn. of *T. mexicanus* for Brzeski, 1998)*T. annulatus* (Cassidy, 1930) Golden, 1971 (nec *T. annulatus* (Merny, 1964) comb. n. (= *T. triversus* nom. nov.))syn. *Tylopharynx annulatus* Cassidy, 1930*Anguillulina annulata* (Cassidy) Goodey, 1932*Chitinotylenchus annulatus* (Cassidy) Filipjev, 1936



**Fig. 104(a).** *Tylenchorhynchus cylindricus* Cobb. A–C. Neotype female obtained from University of California, Davis, USA. D and E. Male from cotton soil, California, USA. A. Head end. B. Tail end of female. C. Entire female. D. Tail end of male. E. Oesophageal region of female. (After M.R. Siddiqi (1972): CIH Descriptions of Plant-parasitic Nematodes.)

- Ditylenchus annulatus* (Cassidy) Sher, 1970  
*Tylenchorhynchus martini* Fielding, 1956
- T. antarcticus* Wouts & Sher, 1981  
 syn. *Dolichorhynchus antarcticus* (Wouts & Sher) Sultan, Singh & Sakhuja, 1991
- T. ascicaudatus* Chang, 1991
- T. aspericutis* Knobloch, 1975
- T. badliensis* Saha & Khan, 1982
- T. bicaudatus* Khakimov, 1973
- T. bohrrensis* Gupta & Uma, 1980
- T. brassicae* Siddiqi, 1961
- T. chirchikensis* Mavlyanov, 1978
- T. chonai* Sethi & Swarup, 1968  
 syn. *Divittus chonai* (Sethi & Swarup) Jairajpuri, 1984  
*Uliginotylenchus chonai* (Sethi & Swarup) Sultan, Singh & Sakhuja, 1991
- T. cicerus* Kakar, Khan & Siddiqi, 1995
- T. clarus* Allen, 1955  
 syn. *Macrorhynchus clarus* (Allen) Sultan, Singh & Sakhuja, 1991  
*Tylenchorhynchus tener* Erzhanova, 1964
- T. clathrocutis* (Lewis & Golden) Fortuner & Luc, 1987  
 syn. *Trilineellus clathrocutis* (Lewis & Golden) Fortuner & Luc, 1987
- T. clavus* F.A. Khan, 1990
- T. claytoni* Steiner, 1937  
 syn. *Tessellus claytoni* (Steiner) Jairajpuri & Hunt, 1984  
*Dolichorhynchus claytoni* (Steiner) Sultan, Singh & Sakhuja, 1991  
*Billineellus claytoni* (Steiner) Volkova, 1993
- T. coffeae* Siddiqi & Basir, 1959  
 syn. *Macrorhynchus coffeae* (Siddiqi & Basir) Sultan, Singh & Sakhuja, 1991
- T. contractus* Loof, 1964  
 syn. *Macrorhynchus contractus* (Loof) Sultan, Singh & Sakhuja, 1991
- T. crassicaudatus* Williams, 1960  
 syn. *Paratrophurus crassicaudatus* (Williams) Andr ssy, 1973  
*Tylenchorhynchus crassicaudatus crassicaudatus* Williams, 1960 (Siddiqi, Mukherjee & Dasgupta, 1982)
- T. crotoni* Pathak & Siddiqui, 1997
- T. cynodoni* Kumar, 1981
- T. dactylurus* Das, 1960  
 syn. *Macrorhynchus dactylurus* (Das) Sultan, Singh & Sakhuja, 1991
- T. delhiensis* Chawla, Bhamburkar, Khan & Prasad, 1968  
 syn. *Macrorhynchus delhiensis* (Chawla *et al.*) Sultan, Singh & Sakhuja, 1991
- T. digitatus* Das, 1960  
 syn. *Macrorhynchus digitatus* (Das) Sultan, Singh & Sakhuja, 1991
- T. dispersus* Siddiqi & Sharma, 1995  
 syn. *T. (Divittus) dispersus* Siddiqi & Sharma, 1995
- T. divittatus* Siddiqi, 1961  
 syn. *Trilineellus divittatus* (Siddiqi) Lewis & Golden, 1981  
*Divittus divittatus* (Siddiqi) Jairajpuri, 1984  
*Morasinema divittatum* (Siddiqi) Javed, 1984

- Uliginotylenchus divittatus* (Siddiqi) Sultan, Singh & Sakhuja, 1991  
*Tylenchorhynchus swatiensis* Nasira, Shahina & Maqbool, 1991; syn. n.
- T. ebriensis* Seinhorst, 1963  
 syn. *Macrorhynchus ebriensis* (Seinhorst) Sultan, Singh & Sakhuja, 1991
- T. elegans* Siddiqi, 1961  
 syn. *Macrorhynchus elegans* (Siddiqi) Sultan, Singh & Sakhuja, 1991  
*Tylenchorhynchus goldeni* Rashid & Singh, 1982  
*Tylenchorhynchus penniseti* Gupta & Uma, 1980  
*Bitylenchus penniseti* (Gupta & Uma) Sultan, Singh & Sakhuja, 1991  
*Tylenchorhynchus punensis* Khan & Darekar, 1979  
*Macrorhynchus punensis* (Khan & Darekar) Sultan, Singh & Sakhuja, 1991  
*Tylenchorhynchus sacchari* Sivakumar & Muthukrishnan, 1983  
*Macrorhynchus sacchari* (Sivakumar & Muthukrishnan) Sultan, Singh & Sakhuja, 1991
- T. eremicolus* Allen, 1955  
 syn. *Macrorhynchus eremicolus* (Allen) Sultan, Singh & Sakhuja, 1991
- T. erevanicus* Karapetjan, 1979 (probably a *Bitylenchus*)
- T. eroshenkoi* Siddiqi, 1986  
 syn. *Tylenchorhynchus varicaudatus* Eroshenko, 1984 (= junior primary homonym of *T. varicaudatus* Singh, 1971)  
*Tylenchorhynchus eroshenkoi* (Eroshenko, 1984) Mahajan & Bello, 1986  
*Tylenchorhynchus helanus* Eroshenko, 1984 (syn. by Brzeski, 1998)
- T. ewingi* Hopper, 1959  
 syn. *Macrorhynchus ewingi* (Hopper) Sultan, Singh & Sakhuja, 1991
- T. fugianensis* Chang, 1990
- T. georgiensis* Eliashvili, 1971
- T. gossypii* Nasira & Maqbool, 1996
- T. graciliformis* Siddiqi & Siddiqui, 1983
- T. haki* Fotedar & Mahajan, 1971  
 syn. *Macrorhynchus haki* (Fotedar & Mahajan) Sultan, Singh & Sakhuja, 1991
- T. hordei* Khan, 1972
- T. iarius* Saha, Gaur & Lal, 1998
- T. impar* Ray & Das, 1983  
 syn. *Divittus impar* (Ray & Das) Mahajan & Bello, 1986  
*Tylenchorhynchus rayi* Fortuner & Luc, 1987 (nom. nov. for *T. impar* Ray & Das, 1983, nec *T. impar* (Khan & Darekar, 1979) Fortuner & Luc, 1987)  
*Uliginotylenchus impar* (Ray & Das) Sultan, Singh & Sakhuja, 1991
- T. irregularis* Wu, 1969
- T. ismaili* Azmi & Ahmad, 1991
- T. kamlae* Shaw & Khan, 1996
- T. kangwoensis* (Geraert, Choi & Choi, 1990) comb. n.  
 syn. *Triversus kangwoensis* Geraert, Choi & Choi, 1990
- T. kashmirensis* Mahajan, 1974
- T. kegasawai* Minagawa, 1995
- T. kegenicus* Litvinova, 1946  
 syn. *Macrorhynchus kegenicus* (Litvinova) Sultan, Singh & Sakhuja, 1991
- T. labiatus* (Jairajpuri, 1984) Siddiqi, 1986

- syn. *Divittus labiatus* Jairajpuri, 1984  
*Uliginotylenchus labiatus* (Jairajpuri) Sultan, Singh & Sakhuja, 1991
- T. latus* Allen, 1955
- T. leucaenus* Azmi, 1991
- T. leviterminalis* Siddiqi, Mukherjee & Dasgupta, 1982  
 syn. *Tylenchorhynchus crassicaudatus leviterminalis* Siddiqi, Mukherjee & Dasgupta, 1982  
*Macrorhynchus leviterminalis* (Siddiqi *et al.*) Sultan, Singh & Sakhuja, 1991  
*Tylenchorhynchus paranudus* Phukan & Sanwal, 1983
- T. madrasensis* Gupta & Uma, 1981  
 syn. *Divittus madrasensis* (Gupta & Uma) Jairajpuri, 1984  
*Uliginotylenchus madrasensis* (Gupta & Uma) Sultan, Singh & Sakhuja, 1991
- T. malinus* Lin, 1992
- T. mangiferae* Luqman & Khan, 1986
- T. manubriatus* Litvinova, 1946  
 syn. *Macrorhynchus manubriatus* (Litvinova) Sultan, Singh & Sakhuja, 1991
- T. mashhoodi* Siddiqi & Basir, 1959  
 syn. *Macrorhynchus mashhoodi* (Siddiqi & Basir) Sultan, Singh & Sakhuja, 1991
- T. mexicanus* Knobloch & Laughlin, 1973
- T. microcephalus* Siddiqi & Patel, 1990
- T. microconus* Siddiqi, Mukherjee & Dasgupta, 1982  
 syn. *Macrorhynchus microconus* (Siddiqi *et al.*) Sultan, Singh & Sakhuja, 1991
- T. minutus* Karapetjan, 1979
- T. musae* Kumar, 1981
- T. neoclavicaudatus* Mathur, Sanwal & Lal, 1979
- T. nordiensis* Khan & Nanjappa, 1974  
 syn. *Tylenchorhynchus aerolatus* Khan & Nanjappa, 1972 (= junior primary homonym of *T. aerolatus* Tobar Jiménez, 1970)  
*Macrorhynchus nordiensis* (Khan & Nanjappa) Sultan, Singh & Sakhuja, 1991
- T. nudus* Allen, 1955  
 syn. *Macrorhynchus nudus* (Allen) Sultan, Singh & Sakhuja, 1991
- T. obscurisulcatus* Andrassy, 1959  
 syn. *Merlinius obscurisulcatus* (Andrassy) Siddiqi, 1970  
*Divittus obscurisulcatus* (Andrassy) Jairajpuri, 1984  
*Trilineellus obscurisulcatus* (Andrassy) Khan & Saeed, 1988  
*Uliginotylenchus obscurisulcatus* (Andrassy) Sultan, Singh & Sakhuja, 1991
- T. oleraceae* Gupta & Uma, 1981  
 syn. *Dolichorhynchus oleraceae* (Gupta & Uma) Sultan, Singh & Sakhuja, 1991  
*Mulkorhynchus* (*Neodolichorhynchus*) *oleraceae* (Gupta & Uma) Volkova, 1993
- T. oryzae* Kaul & Waliullah, 1995
- T. pachys* Thorne & Malek, 1968  
 syn. *Tessellus pachys* (Thorne & Malek) Jairajpuri & Hunt, 1984  
*Dolichorhynchus pachys* (Thorne & Malek) Sultan, Singh & Sakhuja, 1991
- T. paracanalisis* F.A. Khan, 1991
- T. paratriversus* Brzeski, 1992

- T. paulettae* Bloemers & Wanless, 1998  
*T. persicus* Sultan, Singh & Sakhuja, 1991 (perhaps belongs to *Merlinius*)  
*T. phallocercus* Chang, 1991  
*T. projectus* F.A. Khan, 1990  
*T. pruni* Gupta & Uma, 1981  
     syn. *Divittus pruni* (Gupta & Uma) Jairajpuri, 1984  
     *Uliginotylenchus pruni* (Gupta & Uma) Sultan, Singh & Sakhuja, 1991  
*T. robustus* Thorne & Malek, 1968  
     syn. *T. robustoides* Thorne & Malek, 1968 (= objective syn.)  
     *Macrorhynchus robustoides* (Thorne & Malek) Sultan, Singh & Sakhuja, 1991  
*T. sabourensis* Shaw & Khan, 1997  
*T. sanwali* Kumar, 1982  
*T. sculptus* Seinhorst, 1963  
     syn. *Trilineellus sculptus* (Seinhorst) Lewis & Golden, 1981  
     *Divittus sculptus* (Seinhorst) Jairajpuri, 1984  
     *Morasinema sculptum* (Seinhorst) Javed, 1984  
     *Uliginotylenchus sculptus* (Seinhorst) Sultan, Singh & Sakhuja, 1991  
*T. shivanandi* Shaw & Khan, 1992  
*T. siccus* Nobbs, 1990  
*T. silvaticus* Ferris, 1963  
     syn. *Macrorhynchus silvaticus* (Ferris) Sultan, Singh & Sakhuja, 1991  
*T. spinaceai* Singh, 1976 (probably a syn. of *T. brassicae*)  
*T. striatus* Allen, 1955  
     syn. *Macrorhynchus striatus* (Allen) Sultan, Singh & Sakhuja, 1991  
*T. sudanensis* (Decker, Yassin & El-Amin, 1975) Castillo, Siddiqi & Gomez-Barcina, 1989  
     syn. *Paratrophurus sudanensis* Decker, Yassin & El-Amin, 1975  
*T. tarjani* Andr  ssy, 1969  
*T. tenuicauda* Wouts & Sher, 1981  
     syn. *Bitylenchus tenuicauda* (Wouts & Sher) Sultan, Singh & Sakhuja, 1991  
*T. teres* (Khan & Darekar, 1979) Siddiqi, 1986  
     syn. *Telotylenchus teres* Khan & Darekar, 1979  
*T. thermophilus* Golden, Baldwin & Mundo-Ocampo, 1995  
*T. triglyphus* Seinhorst, 1963  
     syn. *Trilineellus triglyphus* (Seinhorst) Lewis & Golden, 1981  
     *Divittus triglyphus* (Seinhorst) Jairajpuri, 1984  
     *Morasinema triglyphus* (Seinhorst) Javed, 1984  
     *Uliginotylenchus triglyphus* (Seinhorst) Sultan, Singh & Sakhuja, 1991  
     *Triversus triglyphus* (Seinhorst) Baujard, Mounport & Martiny, 1995  
*T. trilineatus* Timm, 1963  
     syn. *Uliginotylenchus trilineatus* (Timm) Sultan, Singh & Sakhuja, 1991  
*T. tritici* Golden, Maqbool & Handoo, 1987  
*T. triversus* nom. nov.  
     syn. *Tylenchorhynchus annulatus* (Merny, 1964) comb. n. (= secondary homonym of *T. annulatus* (Cassidy, 1930) Golden, 1971)  
     *Tetylenchus annulatus* Merny, 1964  
     *Triversus annulatus* (Merny, 1964) Sher, 1974



- T. tuberosus* Zarina & Maqbool, 1994  
 syn. *Tylenchorhynchus zarinae* Brzeski & Dolinski, 1998 (was a nom. nov.; original spelling *zarinai*)
- T. variannus* Mavlyanov, 1978
- T. varicaudatus* Singh, 1971  
 syn. *Macrorhynchus varicaudatus* (Singh) Sultan, Singh & Sakhuja, 1991  
*Tylenchorhynchus rosei* Zarina & Maqbool, 1991
- T. vishwanathensis* Pathak & Siddiqui, 1997
- T. yugaensis* (Geraert, Choi & Choi, 1990) comb. n.  
 syn. *Triversus yugaensis* Geraert, Choi & Choi, 1990
- T. zeae* Sethi & Swarup, 1968  
 syn. *Macrorhynchus zeae* (Sethi & Swarup) Sultan, Singh & Sakhuja, 1991

### Species inquirendae

- Tylenchorhynchus alatus* (Cobb, 1930) Filipjev, 1936  
 syn. *Tylenchus alatus* Cobb, 1930  
*Anguillulina alata* (Cobb) Goodey, 1932
- T. browni* (Kreis, 1929) Filipjev & Schuurmans Stekhoven, 1941  
 syn. *Tylenchus browni* Kreis, 1929
- T. bucharicus* (Tulaganov, 1949) Tulaganov, 1954  
 syn. *Anguillulina bucharica* Tulaganov, 1949
- T. caromatae* (Tulaganov, 1949) Tulaganov, 1954  
 syn. *Anguillulina caromatae* Tulaganov, 1949
- T. gadeai* (Arias Delgado, Jiménez Millán & López Pedregal) Braun & Loof, 1966  
 syn. *Pratylenchoides gadeai* Arias Delgado, Jiménez Millán & López Pedregal, 1965
- T. paucus* Kirjanova, 1951
- T. sexamammilatus* (Kirjanova, 1938) Kirjanova, 1961  
 syn. *Anguillulina sexamammilata* Kirjanova, 1938
- T. styriacus* Micoletzky, 1922  
 syn. *Tylenchus* (*Tylenchorhynchus*) *styriacus* (Micoletzky) Filipjev, 1934
- T. symmetricus* (Cobb, 1914) Filipjev, 1936  
 syn. *Tylenchus symmetricus* Cobb, 1914  
*Anguillulina symmetrica* (Cobb) Goodey, 1932
- T. brachycephalus* Litvinova, 1946  
 syn. *Merlinius brachycephalus* (Litvinova) Tarjan, 1973
- T. galeatus* Litvinova, 1946  
 syn. *Merlinius galeatus* (Litvinova) Siddiqi, 1970

### Nomina nuda

- Tylenchorhynchus caricae* Kapoor, 1983
- T. imitans* Kapoor, 1983
- T. robustus* var. *pseudorobustus brasiliensis* Rahm, 1928
- T. stabilis* Kapoor, 1983
- T. sulcaticeps* Kapoor, 1983
- T. valerianae* Kapoor, 1983

ETYMOLOGY. From Greek *tylos* = knob, *enchos* = spear, and *rhynchos* = snout.

The type species was found in brackish soil near a marine estuary, Los Patos, California, USA. A conspectus of *Tylenchorhynchus* spp. is given by Mahajan (1989) and a compendium by Handoo (2000).

### Genus *Bitylenchus* Filipjev, 1934

syn. *Tylenchus* (*Bitylenchus* Filipjev, 1934)

(Figs 104(b), D; 105, A–D; 108(b), E)

### Diagnosis

Telotylenchinae. Small to medium-sized, slender (0.4–1.5 mm long; a = 25–47). Cuticle with fine but distinct annules. Lateral fields each with four incisures, **outer bands areolated**. Deirids absent. Cephalic region finely annulated, usually offset by a constriction or depression and **with lateral longitudinal indentations on lip annules behind amphidial apertures; perioral disc roughly squarish in outline, with six labial sensilla; anteriormost lip annule not six-sectored**. Stylet attenuated or of medium strength, 10–24 µm long; conus tip solid-appearing; rounded basal knobs often sloping backwards. Median bulb well developed, oval, not offset from precorpus by a constriction. Vulva a small transverse slit at 47–61% of body, lips generally modified. Spermathecae round, axial. Ovaries paired. **Postanal intestinal sac large**, filling one-quarter or more of tail cavity, with intestinal granules and fasciculi. Female tail cylindrical, subcylindrical, or subclavate, with rounded usually striated tip; **cuticle at terminus thickened**, but not excessively so. Male tail completely enveloped by bursa. Spicules distally flanged, 19–30 µm long; tip narrow, notched. Gubernaculum **large (10–16 µm long), protrusible**, distally boat-shaped in lateral view, **lacking crest**, titillae or telamon.

### Type species

*Bitylenchus dubius* (Bütschli, 1873) Filipjev, 1934

syn. *Tylenchus dubius* Bütschli, 1873

*Tylenchus* (*Bitylenchus*) *dubius* (Bütschli) Filipjev, 1934

*Anguillulina dubia* (Bütschli) Goodey, 1932

*Tylenchorhynchus dubius* (Bütschli) Filipjev, 1936

*Bitylenchus dubius* (Bütschli) Siddiqi, 1986

### Other species

*Bitylenchus aerolatus* (Tobar Jiménez, 1970) Jairajpuri, 1982

syn. *Tylenchorhynchus aerolatus* Tobar Jiménez, 1970

*Tylenchorhynchus areolatus* Fortuner, 1985 (was an unjustified emendation)

*Bitylenchus aerolatus* (Tobar Jiménez) Siddiqi, 1986

*Bitylenchus intervallatus* (Fortuner & Luc, 1987) comb. n. (nom. nov. for *T. aerolatus* Tobar Jiménez, 1970, nec *T. aerolatus* (Baqri & Jairajpuri, 1969))

*Tylenchorhynchus intervallatus* Fortuner & Luc, 1987

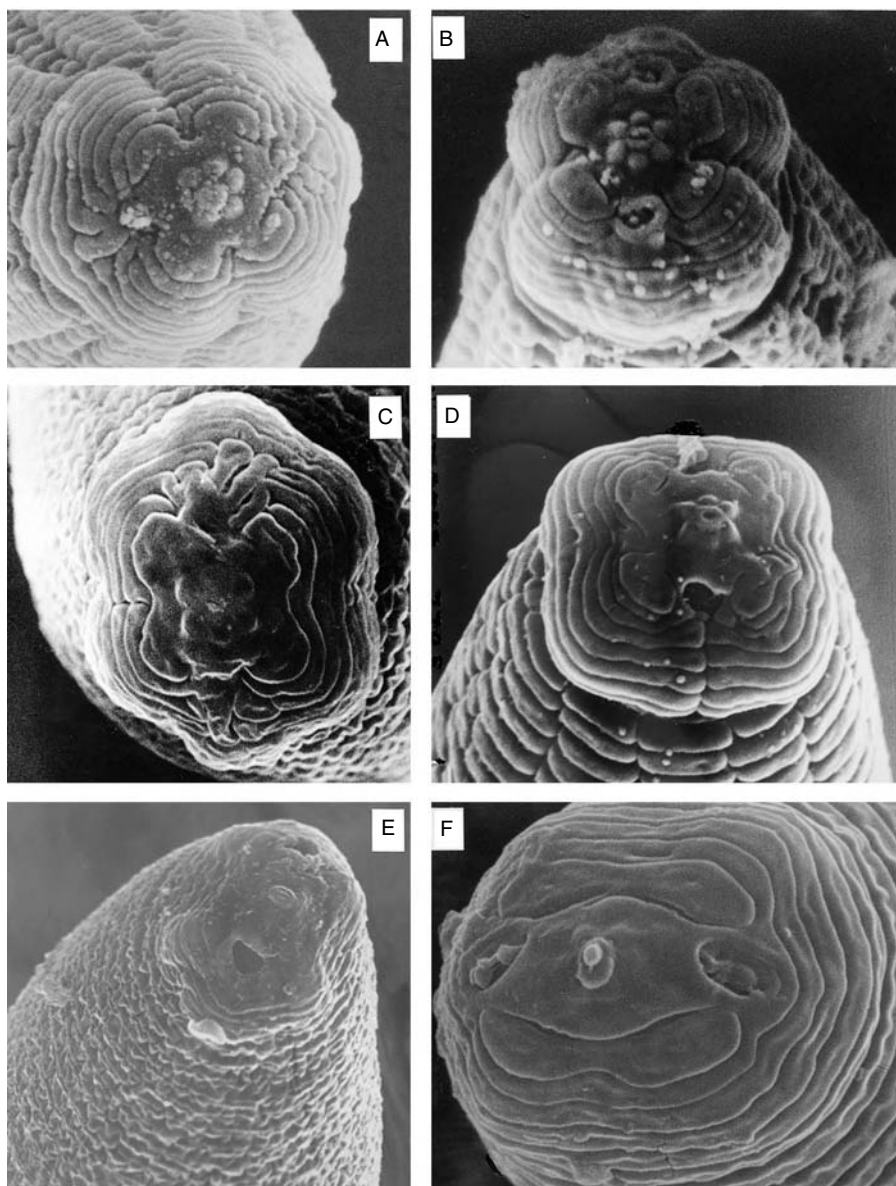
*B. botrys* Siddiqi, 1985

syn. *Tylenchorhynchus* (*Bitylenchus*) *botrys* Siddiqi, 1985

*Bitylenchus botrys* (Siddiqi) Gomez-Barcina, Siddiqi & Castillo, 1992

*B. brevilineatus* (Williams, 1960) Jairajpuri, 1982

syn. *Tylenchorhynchus brevilineatus* Williams, 1960



**Fig. 104(b).** Scanning electron micrographs of female heads. A. *Neodolichorhynchus* (*Neodolichorhynchus*) *microphasmis* (Loof, 1960). B. *Neodolichorhynchus* (*Mulkorhynchus*) *phaseoli* (Sethi & Swarup, 1968). C. *Telotylenchus ventralis* Loof, 1963. D. *Bitylenchus brevilineatus* (Williams, 1960). E. *Meiodorus festonatus* Doucet, 1985. F. *Trichotylenchus falciformis* Whitehead, 1960. (Courtesy P. Baujard, Muséum National d'Histoire Naturelle, Paris.)

- Bitylenchus brevilineatus* (Williams, 1960) Siddiqi, 1986  
*Tylenchorhynchus indicus* Siddiqi, 1961  
*Bitylenchus indicus* (Siddiqi) Siddiqi, 1986
- B. bryobius* (Sturhan, 1966) Jairajpuri, 1982  
 syn. *Tylenchorhynchus bryobius* Sturhan, 1966  
*Bitylenchus bryobius* (Sturhan) Siddiqi, 1986
- B. canalis* (Thorne & Malek, 1968) Jairajpuri, 1982  
 syn. *Tylenchorhynchus canalis* Thorne & Malek, 1968  
*Bitylenchus canalis* (Thorne & Malek) Siddiqi, 1986
- B. clavicaudatus* (Seinhorst, 1963) Siddiqi, 1986  
 syn. *Tylenchorhynchus clavicaudatus* Seinhorst, 1963  
*Tylenchorhynchus clavicauda* Seinhorst, 1968 (= objective syn.)
- B. colombianus* Siddiqi, 1985  
 syn. *Tylenchorhynchus* (*Bitylenchus*) *colombianus* Siddiqi, 1985  
*Bitylenchus colombianus* (Siddiqi) Gomez-Barcina, Siddiqi & Castillo, 1992
- B. cuticaudatus* (Ray & Das, 1983) Siddiqi, 1986  
 syn. *Tylenchorhynchus cuticaudatus* Ray & Das, 1983
- B. depressus* Jairajpuri, 1982  
 syn. *Tylenchorhynchus* (*Bitylenchus*) *depressus* Jairajpuri, 1982  
*Tylenchorhynchus depressus* (Jairajpuri) Golden, Maqbool & Handoo, 1987  
*Bitylenchus depressus* (Jairajpuri) Siddiqi, 1986
- B. equatorialis* Talavera & Siddiqi, 1995
- B. goffarti* (Sturhan, 1966) Jairajpuri, 1982  
 syn. *Tylenchorhynchus goffarti* Sturhan, 1966  
*Bitylenchus goffarti* (Sturhan) Siddiqi, 1986
- B. huesingi* (Paetzold, 1958) Jairajpuri, 1982  
 syn. *Tylenchorhynchus huesingi* Paetzold, 1958  
*Bitylenchus huesingi* (Paetzold) Siddiqi, 1986
- B. iphilus* Minagawa, 1995  
 syn. *Tylenchorhynchus iphilus* (Minagawa) Handoo, 2000
- B. kidwaii* (Rashid & Heyns, 1990) comb. n.  
 syn. *Tylenchorhynchus kidwaii* Rashid & Heyns, 1990
- B. mediocris* Talavera & Siddiqi, 1995
- B. natalensis* (Kleynhans, 1984) Siddiqi, 1986  
 syn. *Tylenchorhynchus natalensis* Kleynhans, 1984
- B. parvus* (Allen, 1955) Jairajpuri, 1982  
 syn. *Tylenchorhynchus parvus* Allen, 1955  
*Bitylenchus parvus* (Allen) Siddiqi, 1986
- B. quaidi* (Golden, Maqbool & Handoo, 1987) comb. n.  
 syn. *Tylenchorhynchus quaidi* Golden, Maqbool & Handoo, 1987  
*Tylenchorhynchus allii* Khurma & Mahajan, 1988  
*Bitylenchus allii* (Khurma & Mahajan) comb. n.
- B. queirozi* (Monteiro & Lordello, 1976) Jairajpuri, 1982  
 syn. *Tylenchorhynchus queirozi* Monteiro & Lordello, 1976  
*Bitylenchus queirozi* (Monteiro & Lordello) Siddiqi, 1986
- B. serranus* Gomez-Barcina, Siddiqi & Castillo, 1992
- B. singularis* Siddiqi & Sharma, 1994

- B. swarupi* (Singh & Khera, 1978) Jairajpuri, 1982  
 syn. *Tylenchorhynchus swarupi* Singh & Khera, 1978  
*Bitylenchus swarupi* (Singh & Khera) Siddiqi, 1986
- B. teeni* (Hashim, 1984) Siddiqi, 1986  
 syn. *Tylenchorhynchus teeni* Hashim, 1984
- B. tobari* (Sauer & Annells, 1981) Siddiqi, 1986  
 syn. *Tylenchorhynchus tobari* Sauer & Annells, 1981
- B. usmanensis* (Khurma & Mahajan, 1988) comb. n.  
 syn. *Tylenchorhynchus usmanensis* Khurma & Mahajan, 1988
- B. ventrosignatus* (Tobar Jiménez, 1969) Jairajpuri, 1982  
 syn. *Tylenchorhynchus ventrosignatus* Tobar Jiménez, 1969  
*Bitylenchus ventrosignatus* (Tobar Jiménez) Siddiqi, 1986
- B. vulgaris* (Upadhyay, Swarup & Sethi, 1972) Jairajpuri, 1982  
 syn. *Tylenchorhynchus vulgaris* Upadhyay, Swarup & Sethi, 1972 (syn. of *T. brevilineatus* for Khan & Khan, 1997)  
*Bitylenchus vulgaris* (Upadhyay, Swarup & Sethi) Siddiqi, 1986
- B. zambiensis* (Venditti & Noel, 1995) comb. n.  
 syn. *Tylenchorhynchus zambiensis* Venditti & Noel, 1995

## Notes

*Bitylenchus* was proposed by Filipjev (1934a) as one of the five subgenera of *Tylenchus* Bastian, 1865; the other four being *Anguillulina* Gervais & Van Beneden, 1859; *Chitinotylenchus* Micoletzky, 1922; *Tylenchorhynchus* Cobb, 1913; and *Tylenchus*, *sensu stricto*. The five subgenera were compared in a key, in which *Tylenchus dubius* Bütschli, 1873, was mentioned as the type species of *Bitylenchus*. This is an indication that the species name *dubius* was combined with *Bitylenchus*. Filipjev (1936) synonymized the subgenus *Bitylenchus* with *Tylenchorhynchus* Cobb, 1913. Jairajpuri (1982) referred to Siddiqi & Jairajpuri (1982) for the resurrection of *Bitylenchus* and the transfer of certain species of *Tylenchorhynchus* to that genus, but Siddiqi & Jairajpuri's (1982) paper was never published. Jairajpuri (1982) described a new species, *Tylenchorhynchus* (*Bitylenchus*) *depressus*, and gave a key to the species of the subgenus *Bitylenchus*. By this action, Jairajpuri (1982) is deemed to have transferred the species given under the key to the genus *Bitylenchus*, on the principle of coordination.

*Bitylenchus* is similar to *Sauertylechus* Sher, 1974 except for the differences in the structure of the lip region and elongation of the stylet (see discussion under *Sauertylechus*). *Bitylenchus* differs from *Tylenchorhynchus* in having outer bands of lateral fields areolated, a large postanal intestinal sac containing intestinal granules and fasciculi, relatively more thickened cuticle at female tail tip, and gubernaculum lacking a crest (see Gomez-Barcina *et al.*, 1992).

Fortuner & Luc (1987) did not recognize *Bitylenchus* on the grounds that it 'was defined using very secondary characteristics that are not known for many taxa, and that, when known, do not clearly differentiate the genus from *Tylenchorhynchus*'. They assigned *Sauertylechus*, a close relative of *Bitylenchus*, to Belonolaiminae, emphasizing the well-marked, round perioral disc and elongate stylet. Gomez-Barcina *et al.* (1992) elaborately discussed the validity of *Bitylenchus* and its relationship to *Sauertylechus*.

ETYMOLOGY. From Latin *bis* = two (for two ovaries), and *Tylenchus*.

The type species was described by Bütschli (1873) as *Tylenchus dubius* on a male collected around roots of *Centaurea cyanus* L., near Frankfurt-am-Main, Germany. It is a widely distributed species in lighter soils of Europe and an obligatory root ectoparasite of higher plants and is damaging to field crops such as green pea, sorghum, turnip and wheat (Sharma, 1971).

### Genus *Sauertylenchus* Sher, 1974

(Fig. 105, E–H)

#### Diagnosis

Telotylenchinae. Medium-sized (1.4–2 mm), slender. Annules distinct. Lateral fields each with four incisures, **outer bands incompletely areolated**. Deirids absent. **Cephalic region offset, annulated, divided into six sectors anteriorly, labial disc round, distinct**; framework weakly sclerotized. Stylet long (33–40  $\mu\text{m}$ ), very slender, conus appearing solid anteriorly, knobs small and rounded. Median bulb oval. Basal bulb saccate, rounded posteriorly; cardia large. **Intestine with fasciculi extending into tail cavity**. Female tail subcylindrical, over two anal body widths long (2.4–3.2 anal body widths long in type species). Male tail enveloped by a simple crenate bursa. Spicules with large distal flanges, 33–38  $\mu\text{m}$  long in type species. Gubernaculum large, with titillae, recurved distally. Hypoptygma absent.

#### Type species

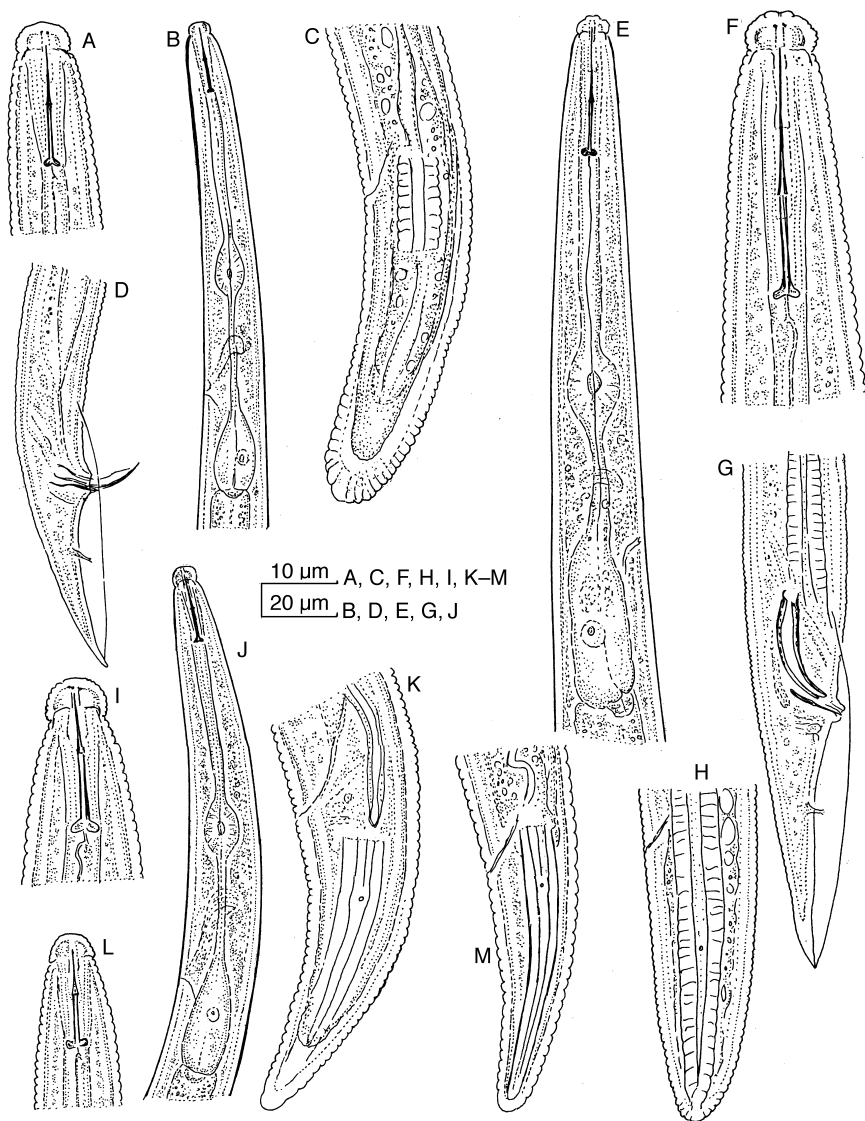
*Sauertylenchus labiodiscus* Sher, 1974

#### Other species

- Sauertylenchus ibericus* (Mahajan & Nombela, 1987) comb. n.  
syn. *Tylenchorhynchus ibericus* Mahajan & Nombela, 1987
- S. maximus* (Allen, 1955) comb. n.  
syn. *Tylenchorhynchus maximus* Allen, 1955  
*Bitylenchus maximus* (Allen) Siddiqi, 1986  
*Tylenchorhynchus wilskii* Kornobis, 1980 (syn. of *T. maximus* for Brzeski, 1998)  
*Bitylenchus wilskii* (Kornobis) Jairajpuri, 1982  
*Bitylenchus wilskii* (Kornobis) Siddiqi, 1986
- S. pratensis* (Gomez-Barcina, Siddiqi & Castillo, 1992) comb. n.  
syn. *Bitylenchus pratensis* Gomez-Barcina, Siddiqi & Castillo, 1992  
*Tylenchorhynchus pratensis* (Gomez-Barcina *et al.*) Baujard, Mounport & Martiny, 1994
- S. velatus* (Sauer & Annells, 1981) comb. n.  
syn. *Tylenchorhynchus velatus* Sauer & Annells, 1981  
*Bitylenchus velatus* (Sauer & Annells) Sultan, Singh & Sakhuja, 1991  
*Bitylenchus velatus* (Sauer & Annells) Gomez-Barcina, Siddiqi & Castillo, 1992

#### Notes

Sher (1974) proposed the genus *Sauertylenchus* and placed it in the Tylenchorhynchinae. He stated that its type species *Sauertylenchus labiodiscus* Sher,



**Fig. 105.** A–D. *Bitylenchus dubius* (Bütschli) from Scotland. E–H. *Sauertylenchus labiodiscus* Sher, paratypes. I–K. *Quinisulcius solani* Maqbool, paratypes (= *Q. capitatus* (Allen)). L and M. *Quinisulcius acutus* (Allen), paratype. D, F and G. Males, remainder females. A, F, I and L. Head ends. B, E and J. Oesophageal regions. C, D, G, H, K and M. Tail ends.

1974 shared characters, such as a set-off cephalic region with a distinct labial disc and a long thin stylet, with *Geocenamus* of the subfamily Merliniinae, but because of the four incisures in the lateral field and the shapes of the spicules and gubernaculum, he placed it in the Tylenchorhynchinae. He stated that the two subfamilies

were well defined (Siddiqi, 1971). Fortuner & Luc (1987), however, synonymized Merliniinae with Telotylenchinae (= Tylenchorhynchinae) and assigned *Sauertylenchus* and *Geocenamus* to Belonolaiminae.

Gomez-Barcina *et al.* (1992) gave reasons for accepting Merliniinae as a well-defined group, separate from the Telotylenchinae, and for regarding *Sauertylenchus* and *Geocenamus* to belong in the Telotylenchinae and Merliniinae, respectively. They agreed with Siddiqi (1986) that *Sauertylenchus* is similar to *Bitylenchus* except for the difference in the structure of the lip region which has an offset labial disc and the first cephalic annule divided into six sectors (= lip areas) and a relatively longer stylet. They provided SEM face views of *Bitylenchus maximus* and *B. pratensis* which also showed an offset labial disc surrounded by six lip areas. A similar face view is seen in *B. velatus* and Mahajan & Nombela (1987) had noted that in *Tylenchorhynchus ibericus* the labial disc was reminiscent of that in *Sauertylenchus labiodiscus* Sher, 1974. In all these species the stylet is 20  $\mu\text{m}$  or more in length. In *Bitylenchus*, on the contrary, the labial disc is indistinct, four-lobed and not offset and the first cephalic annule is not divided into six sectors (see Sher & Bell (1975) and Gomez-Barcina *et al.* (1992)). It is, therefore, justified to shift *Bitylenchus maximus*, *B. pratensis*, *B. velatus* and *B. ibericus* to *Sauertylenchus* (a parallel can be seen in *Merlinius* vs. *Geocenamus* where labial structures and the elongation of the stylet are used as distinguishing characters).

ETYMOLOGY. Patronym, a compound name, prefix after M.R. Sauer, and Greek *tylos* = knob, *enchos* = spear.

The type species was found around roots of *Rhagodia* sp. in New South Wales, Australia.

### Genus *Quinisulcius* Siddiqi, 1971

(Fig. 105, I–M)

#### Diagnosis

Telotylenchinae. Small-sized (0.47–0.9 mm), strongly curving when relaxed. Annules prominent. **Lateral fields each with five incisures**, smooth or partially areolated. Deirids absent. Cephalic region offset, rounded, finely annulated; labial disc indistinct; framework with light to moderate sclerotization. Stylet moderately strong, 12–24  $\mu\text{m}$  long (16–19  $\mu\text{m}$  long in type species); conus appearing solid anteriorly; knobs rounded, rarely cupped anteriorly. Median bulb well developed, oval, not offset from precorpus by a constriction. Basal bulb large, usually offset from intestine. Cardia prominent. Vulva at 51–59%, lips not modified. Spermathecae round, axial or slightly offset, rarely functional. Ovaries paired, outstretched. Female tail conoid, usually ventrally arcuate, terminal annule enlarged, smooth or striated. **Males rare or absent.** Bursa well developed, simple, enveloping entire tail. Spicules arcuate, with poorly developed distal flanges, 14–24  $\mu\text{m}$  long. Gubernaculum modified, with proximal end directed dorsally.



## Type species

- Quinisulcius capitatus* (Allen, 1955) Siddiqi, 1971  
 syn. *Tylenchorhynchus capitatus* Allen, 1955  
*Tylenchorhynchus acti* Hopper, 1959  
*Q. acti* (Hopper) Siddiqi, 1971  
*Tylenchorhynchus nilgiriensis* Seshadri, Muthukrishnan & Shunmugam, 1967  
*Q. nilgiriensis* (Seshadri *et al.*) Siddiqi, 1971  
*Quinisulcius himalayae* Mahajan, 1974  
*T. himalayae* (Mahajan) Fortuner & Luc, 1987  
*Quinisulcius solani* Maqbool, 1982  
*T. solani* (Maqbool) Fortuner & Luc, 1987  
*Tylenchorhynchus maqbooli* Mizukubo, Toida & Keereevan, 1993 (nom. nov.  
 for *T. solani* (Maqbool, 1982), nec *T. solani* Gupta & Uma, 1981)  
*Quinisulcius paracti* Ray & Das, 1983  
*T. paracti* (Ray & Das) Fortuner & Luc, 1987

## Other species

- Quinisulcius acutoides* (Thorne & Malek, 1968) Siddiqi, 1971  
 syn. *Tylenchorhynchus acutoides* Thorne & Malek, 1968  
*Q. acutus* (Allen, 1955) Siddiqi, 1971  
 syn. *Tylenchorhynchus acutus* Allen, 1955  
*Tetylenchus hanumanthi* Edward, Uma & Sharma, 1983  
*Quinisulcius hanumanthi* (Edward, Uma & Sharma, 1983) comb. n.  
*Q. brevistyletus* Kulinich, 1985  
 syn. *Tylenchorhynchus brevistyletus* (Kulinich) Ebsary, 1991  
*Q. cacti* (Chawla, Bhamburkar, Khan & Prasad, 1968) Siddiqi, 1971  
 syn. *Tylenchorhynchus cacti* Chawla, Bhamburkar, Khan & Prasad, 1968  
*Q. curvus* (Williams, 1960) Siddiqi, 1971  
 syn. *Tylenchorhynchus curvus* Williams, 1960  
*Q. domesticus* Sultan, Singh & Sakhuja, 1995  
*Q. gundariensis* Khan & Singh, 1999  
*Q. indicus* Luqman & Khan, 1986  
 syn. *Tylenchorhynchus indicatus* Ebsary, 1991 (nom. nov. for *Tylenchorhynchus indicus* (Luqman & Khan, 1986) comb. n., nec *T. indicus* Siddiqi)  
*Q. lineatus* Karapetjan, 1979  
 syn. *Tylenchorhynchus lineatus* (Karapetjan, 1979) Fortuner & Luc, 1987  
*Q. obregonus* Knobloch & Laughlin, 1973  
 syn. *Tylenchorhynchus obregonus* (Knobloch & Laughlin, 1973) Fortuner & Luc, 1987  
*Q. punici* Gupta & Uma, 1980  
 syn. *Tylenchorhynchus punici* (Gupta & Uma) Fortuner & Luc, 1987  
*Q. quaidi* Zarina & Maqbool, 1992  
 syn. *Tylenchorhynchus pakistanensis* Brzeski & Dolinski, 1998 (was nom. nov. for  
*Q. quaidi* Zarina & Maqbool, 1992 (= *T. quaidi*), nec *T. quaidi* Golden,  
 Maqbool & Handoo, 1987)  
*Q. rotundicephalus* Shaw & Khan, 1997  
*Q. tarjani* Knobloch, 1975

syn. *Tylenchorhynchus tarjani* (Knobloch, 1975) Fortuner & Luc, 1987  
*Tylenchorhynchus knoblochi* Fortuner & Luc, 1987 (nom. nov. for  
*Tylenchorhynchus tarjani* (Knobloch, 1975), nec *T. tarjani* Andr ssy, 1969)

ETYMOLOGY. Latin *quini* = five, and *sulci* = furrows (for incisures of lateral field).

The type species was collected from pear soil in an orchard near Watsonville, California, USA.

### **Genus *Neodolichorhynchus* Jairajpuri & Hunt, 1984**

syn. ***Dolichorhynchus* Mulk & Jairajpuri, 1974 (a primary homonym of *Dolichorhynchus* Willey, 1901, Cephalochordata)**  
***Prodolichorhynchus* Jairajpuri, 1985**  
***Mulkorhynchus* Jairajpuri, 1988**  
***Billineellus* Volkova, 1993**

### Diagnosis

Telotylenchinae. Small-sized (under 1 mm), ventrally arcuate or more strongly curved upon relaxation. Annules prominent, marked by deep transverse striae. **Cuticle with 6–14 longitudinal ridges or lamellae** outside lateral fields. Lateral fields each with **one** (two incisures) or **three ridges** (four incisures), variably areolated. Cephalic region rounded **with dorsal and ventral indentations** (except *D. lamelliferus*), offset (continuous with body in *D. lamelliferus*); finely annulated; labial disc indistinct; framework with light to moderate sclerotization. Stylet about 12–27  $\mu\text{m}$  long, conus solid-appearing in anterior third. Median bulb round to oval, with prominent refractive thickenings. Basal bulb offset from intestine; cardia prominent, rounded. Deirids absent. Vulva median or submedian, with or without minute lateral membranes. Spermathecae axial, rounded. Ovaries paired, outstretched. Female tail conoid to subcylindroid, ending in a rounded, often lobe-like, hyaline terminus. Male tail enveloped by a large bursa, which may or may not be doubly notched or indented at tail terminus to appear trilobed in dorso-ventral view. Spicules with distal flanges. Gubernaculum large, protrusible. Mostly inhabitants of sandy soils.

### Type subgenus

*Neodolichorhynchus* Jairajpuri & Hunt, 1984

### Other subgenera

*Mulkorhynchus* Jairajpuri, 1988  
*Prodolichorhynchus* Jairajpuri, 1985

### Note

The subgeneric categories help in understanding the inter-relatedness of species. The citation of a subgenus name within brackets between the genus and the species name neither affects the binomen nor makes the name a trinomen. For example, the name *Neodolichorhynchus* (*Prodolichorhynchus*) *elegans* (Germani & Luc, 1984) is the same as *Neodolichorhynchus elegans*. However, the name *Neodolichorhynchus*

(*Prodolichorhynchus*) *elegans* does indicate that the species epithet *elegans* has been combined with *Prodolichorhynchus*.

### Key to subgenera of *Neodolichorhynchus*

1. Lateral field with a single ridge ..... *Prodolichorhynchus*  
     Lateral field with three ridges ..... 2
2. Vulva with minute lateral cuticular membranes; bursa generally notched  
     at tail tip ..... *Mulkorhynchus*  
     Vulva without lateral cuticular membranes; bursa not notched at  
     tail tip ..... *Neodolichorhynchus*

### Subgenus *Neodolichorhynchus* Jairajpuri & Hunt, 1984

(Figs 104(b)A; 106, A–C)

#### Diagnosis

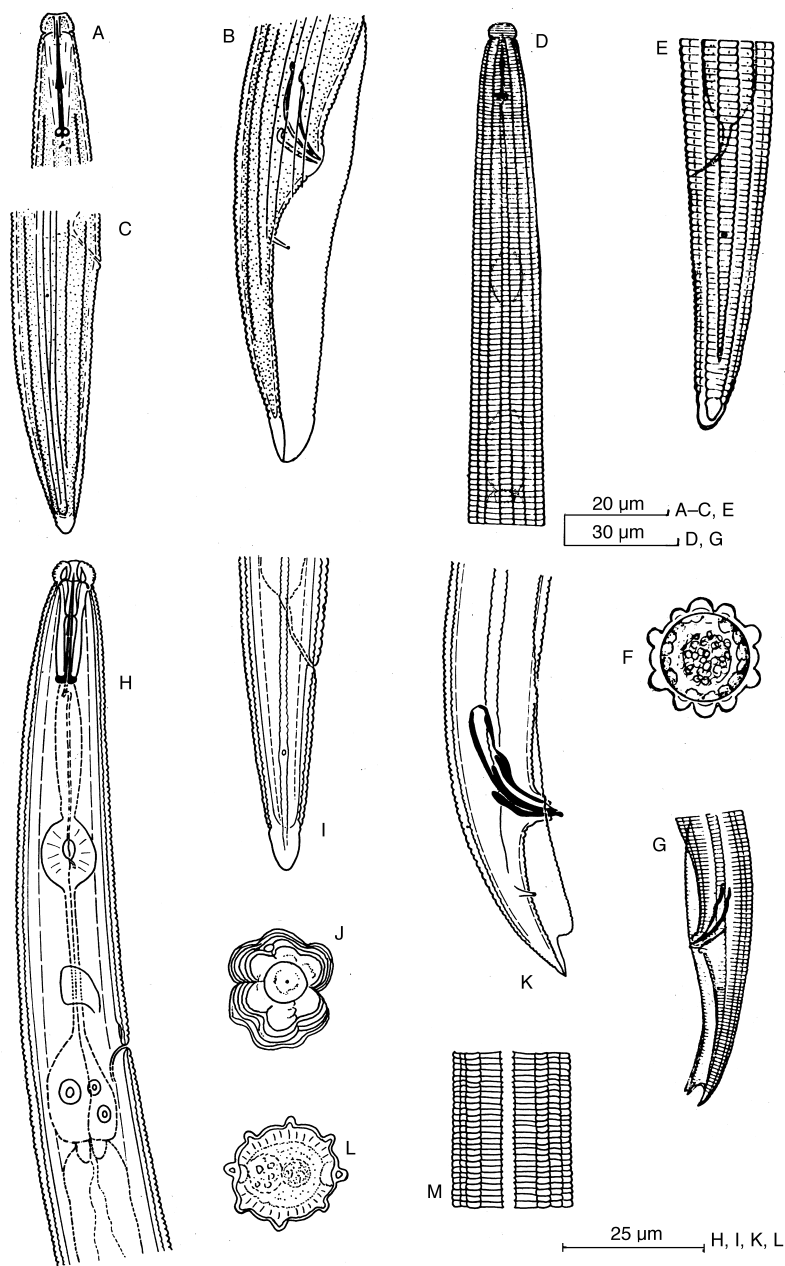
Genus *Neodolichorhynchus*. Lateral fields irregularly areolated; with three ridges which are higher than other body ridges. Cephalic region offset from body, dorso-ventrally indented; **annules behind amphidial pores broken**. Vulva lacking lateral cuticular membranes. **Bursa not notched at tail tip**. Gubernaculum with smooth proximal end.

#### Type species

- Neodolichorhynchus* (*Neodolichorhynchus*) *microphasmis* (Loof, 1960) Jairajpuri & Hunt, 1984  
 syn. *Tylenchorhynchus microphasmis* Loof, 1960  
*Dolichorhynchus microphasmis* (Loof) Mulk & Siddiqi, 1982  
*Neodolichorhynchus microphasmis* (Loof) Jairajpuri & Hunt, 1984  
*Mulkorhynchus* (*Neodolichorhynchus*) *microphasmis* (Loof) Volkova, 1993  
*Tylenchorhynchus pini* Kulinich, 1985  
*Neodolichorhynchus pini* (Kulinich, 1985) comb. n.

#### Other species

- Neodolichorhynchus* (*Neodolichorhynchus*) *bicostatus* Talavera & Tobar, 1997  
*N. (N.) cristatus* (Ivanova, 1983) Siddiqi, 1986  
 syn. *Tylenchorhynchus cristatus* Ivanova, 1983  
*Dolichorhynchus* (*N.*) *cristatus* (Ivanova, 1983) Siddiqi, 1986  
*N. (N.) gladiolatus* (Fortuner & Amougou, 1973) Jairajpuri & Hunt, 1984  
 syn. *Tylenchorhynchus gladiolatus* Fortuner & Amougou, 1973  
*D. gladiolatus* (Fortuner & Amougou) Mulk & Siddiqi, 1982  
*N. (N.) judithae* (Andrássy, 1962) Jairajpuri & Hunt, 1984  
 syn. *Tylenchorhynchus judithae* Andrássy, 1962  
*D. judithae* (Andrássy) Mulk & Siddiqi, 1982  
*N. (N.) novenus* (Nobbs, 1990) comb. n.  
 syn. *Tylenchorhynchus novenus* Nobbs, 1990  
*N. (N.) solani* (Gupta & Uma, 1981) Siddiqi, 1986



**Fig. 106.** A–C. *Neodolichorhynchus* (*Neodolichorhynchus*) *microphasmis* (Loof). D–G. *Neodolichorhynchus* (*Mulkorhynchus*) *phaseoli* (Sethi & Swarup). H–M. *Neodolichorhynchus* (*Prodolichorhynchus*) *elegans* (Germani & Luc). A. Head end of female. B, K and G. Tail ends of males. C, E and I. Tail ends of females. D and H. Oesophageal regions of females. F and L. Cross-sections at midbody. J. *En face* view. M. Cuticular pattern at midbody. (A–C. After Loof (1960). D–G. Redrawn after Mulk & Jairjuri (1972). H–M. After Germani & Luc (1984).)

- syn. *Tylenchorhynchus solani* Gupta & Uma, 1981  
*Bitylenchus solani* (Gupta & Uma) Jairajpuri, 1982  
*D. (N.) solani* (Gupta & Uma) Siddiqi, 1986  
*N. (N.) sulcatus* (de Guiran, 1967) Jairajpuri & Hunt, 1984  
 syn. *Tylenchorhynchus sulcatus* de Guiran, 1967  
*D. sulcatus* (de Guiran) Mulk & Siddiqi, 1982

ETYMOLOGY. From Greek *neos* = young, new, and *Dolichorhynchus*.

The type species was collected from sandy soil, Westerbork, The Netherlands. Keys to species of *Neodolichorhynchus* and *Mulkorhynchus* (= *Dolichorhynchus*) have been provided by Jairajpuri and Hunt (1984).

### **Subgenus *Mulkorhynchus* Jairajpuri, 1988**

**syn. *Dolichorhynchus* Mulk & Jairajpuri, 1974 (a primary homonym of *Dolichorhynchus* Willey, 1901, Cephalochordata)**

(Figs 104(b), B; 106, D–G)

#### **Diagnosis**

Genus *Neodolichorhynchus*. Lateral fields completely areolated; their ridges about as high as other body ridges. Cephalic region offset from body (rarely continuous), dorso-ventrally indented (except *D. lamelliferus*); **annules behind amphidial pores not broken. Vulva with minute lateral cuticular membranes. Bursa doubly notched at tail tip** (except occasionally in *D. lamelliferus*). Gubernaculum usually with projections at proximal end.

#### **Type species**

*Mulkorhynchus phaseoli* (Sethi & Swarup, 1968) Jairajpuri, 1988

#### **Present status**

*Neodolichorhynchus (Mulkorhynchus) phaseoli* (Sethi & Swarup, 1968) Talavera & Tobar, 1997

syn. *Tylenchorhynchus phaseoli* Sethi & Swarup, 1968

*Dolichorhynchus phaseoli* (Sethi & Swarup) Mulk & Jairajpuri, 1974

#### **Other species**

*Neodolichorhynchus (Mulkorhynchus) estherae* (Kleynhans, 1992) comb. n.

syn. *Tylenchorhynchus estherae* Kleynhans, 1992

*N. (M.) lamelliferus* (de Man, 1880) Volkova, 1993

syn. *Tylenchus lamelliferus* de Man, 1880

*Anguillulina lamellifera* (de Man) Goodey, 1932

*Tylenchorhynchus lamelliferus* (de Man) Filipjev, 1936

*Dolichorhynchus lamelliferus* (de Man) Mulk & Siddiqi, 1982

*M. lamelliferus* (de Man) Jairajpuri, 1988

*M. (Neodolichorhynchus) lamelliferus* (de Man) Volkova, 1993

*N. lamelliferus* (de Man) Talavera & Tobar, 1997

*N. (M.) motiaii* (Zarina & Maqbool, 1998) comb. n.

- syn. *Dolichorhynchus* (*Dolichorhynchus*) *motiaii* Zarina & Maqbool, 1998  
*Tylenchorhynchus motiaii* (Zarina & Maqbool) Brzeski, 1998  
 N. (M.) *nigericus* (Mulk & Jairajpuri, 1974) Volkova, 1993  
 syn. *Dolichorhynchus nigericus* Mulk & Jairajpuri, 1974  
*Tylenchorhynchus nigericus* (Mulk & Jairajpuri) Fortuner & Luc, 1987  
*M. nigericus* (Mulk & Jairajpuri) Jairajpuri, 1988  
*M. (Neodolichorhynchus) nigericus* (Mulk & Jairajpuri) Volkova, 1993  
*N. nigericus* (Mulk & Jairajpuri) Talavera & Tobar, 1997  
 N. (M.) *parvus* (Mulk & Siddiqi, 1983) Talavera & Tobar, 1997  
 syn. *Dolichorhynchus parvus* Mulk & Siddiqi, 1983  
*Tylenchorhynchus parvus* (Mulk & Siddiqi) Fortuner & Luc, 1987  
*Tylenchorhynchus mulki* Fortuner & Luc, 1987 (nom. nov. for *T. parvus* (Mulk & Siddiqi), nec *T. parvus* Allen, 1955)  
*M. parvus* (Mulk & Siddiqi) Jairajpuri, 1988  
 N. (M.) *prophasmsis* (Jairajpuri & Hunt, 1984) Talavera & Tobar, 1997  
 syn. *Dolichorhynchus prophasmsis* Jairajpuri & Hunt, 1984  
*Tylenchorhynchus prophasmsis* (Jairajpuri & Hunt) Fortuner & Luc, 1987  
*M. prophasmsis* (Jairajpuri & Hunt) Jairajpuri, 1988  
 N. (M.) *tuberosus* (Maqbool, Ghazala & Fatima, 1984) Talavera & Tobar, 1997  
 syn. *Dolichorhynchus tuberosus* Maqbool, Ghazala & Fatima, 1984  
*Tylenchorhynchus tuberosus* (Maqbool et al.) Fortuner & Luc, 1987  
*M. tuberosus* (Maqbool et al.) Jairajpuri, 1988

#### Note

Volkova (1993) proposed the combinations *Mulkorhynchus* (*Neodolichorhynchus*) *lamelliferus* (de Man, 1880) Volkova, 1993 and *M. (Neodolichorhynchus) nigericus* (Mulk & Jairajpuri) Volkova, 1993. This implies that Volkova did propose the combinations of the two species with *Mulkorhynchus* as well as with *Neodolichorhynchus*.

ETYMOLOGY. Patronym honouring M.M. Mulk, and suffix of *Tylenchorhynchus*.

The type species was originally collected around roots of *Phaseolus aconitifolius* Jacq. at Bhatinda, Punjab State, India.

#### Subgenus *Prodolichorhynchus* Jairajpuri, 1985

syn. *Billineellus* Volkova, 1993

(Fig. 106, H–M)

#### Diagnosis

Genus *Neodolichorhynchus*. Cuticle with eight longitudinal ridges including two lateral field ridges. **Lateral field in the form of a single ridge** which is slightly higher than other ridges, not areolated. Cephalic region offset from body, dorso-ventrally indented. **Bursa with double depressions at tail tip.**

#### Type species

*Prodolichorhynchus elegans* (Germani & Luc, 1984) Jairajpuri, 1985

## Present status

*Neodolichorhynchus* (*Prodolichorhynchus*) *elegans* (Germani & Luc, 1984) comb. n.

syn. *Dolichorhynchus elegans* Germani & Luc, 1984

*Prodolichorhynchus elegans* (Germani & Luc) Jairajpuri, 1985

*Tylenchorhynchus elegans* (Germani & Luc) Fortuner & Luc, 1987

*Tylenchorhynchus germanii* Fortuner & Luc, 1987 (nom. nov. for *T. elegans* (Germani & Luc), nec *T. elegans* Siddiqi, 1961)

*Billineellus elegans* (Germani & Luc) Volkova, 1993

No other species.

ETYMOLOGY. From Greek *pro* = before, forward, and *Dolichorhynchus*.

The type species was collected from around the roots of *Arachis hypogaea* at Patar, Senegal.

**Genus *Uliginotylenchus* Siddiqi, 1971**

(Fig. 103, J–N)

## Diagnosis

Telotylenchinae. Body 0.4–1 mm long, slender ( $a = 25\text{--}50$ ), arcuate to more curved when relaxed. Annules prominent, smooth. **Lateral field with three incisures, areolated.** Deirids absent. Cephalic region elevated, continuous or slightly offset, finely but distinctly annulated; labial disc indistinct; framework moderately sclerotized. Stylet attenuated, 14–27.5  $\mu\text{m}$  long (14–16  $\mu\text{m}$  long in type species); conus solid-appearing for most of its length; knobs small, rounded. **Vulva in a body cavity or depression, with small epiptygma. Spermathecae pouch-like, usually offset. Female tail elongate-subclavate to cylindroid, with a broadly rounded, usually annulated terminus and over 25 (usually 30–40) annules.** Males known for all nominal species. Spicules with large distal flanges, 18–30  $\mu\text{m}$  long. **Gubernaculum 8–12  $\mu\text{m}$  long, rod-like, protrusible, with proximal portion directed dorsally. Found around roots in marsh or very wet soils.**

## Type species

*Uliginotylenchus uliginosus* (Siddiqi, 1970) Siddiqi, 1971

syn. *Tylenchorhynchus uliginosus* Siddiqi, 1970

*Trichotylenchus uliginosus* (Siddiqi) Seinhorst, 1971

## Other species

*Uliginotylenchus astriatus* (Khan & Nanjappa, 1971) Siddiqi, 1986

syn. *Trichotylenchus astriatus* Khan & Nanjappa, 1971

*Trichotylenchus trilokiae* Singh, 1971

*Uliginotylenchus trilokiae* (Singh) Siddiqi, 1986

*U. bifasciatus* (Andrássy, 1961) Siddiqi, 1971

syn. *Tylenchorhynchus bifasciatus* Andrássy, 1961

*Trichotylenchus bifasciatus* (Andrássy) Fortuner & Luc, 1987

*U. cylindricaudatus* Liu, Duan & Liu, 1993

*U. palustris* (Merny & Germani, 1968) Siddiqi, 1971

- syn. *Tylenchorhynchus palustris* Merny & Germani, 1968  
*Trichotylenchus palustris* (Merny & Germani) Seinhorst, 1971  
*U. papyrus* (Siddiqi, 1970) Siddiqi, 1971  
 syn. *Tylenchorhynchus papyrus* Siddiqi, 1970  
*Trichotylenchus papyrus* (Siddiqi) Seinhorst, 1971  
*U. rhopalocercus* (Seinhorst, 1963) Siddiqi, 1971  
 syn. *Tylenchorhynchus rhopalocercus* Seinhorst, 1963  
*Trichotylenchus rhopalocercus* (Seinhorst) Seinhorst, 1971

ETYMOLOGY. From Latin *uliginosus* = marshy, and *Tylenchus*.

The type species was collected from swampy soil near a fish pond in Kabanyolo, near Kampala, Uganda. Castillo *et al.* (1989) and Liu *et al.* (1993) have provided keys to species of *Uliginotylenchus*.

### Genus *Paratrophurus* Arias, 1970

(Fig. 107, A–E)

#### Diagnosis

Telotylenchinae. Body 0.5–1.2 mm long. Annules distinct, smooth. Lateral field with four incisures, not areolated. Deirids absent. Phasmids at or anterior to middle of tail. **Cephalic region narrow, conoid-rounded, apparently smooth**, circular in cross-section; labial disc indistinct; framework moderately to strongly sclerotized. Stylet moderately strong, 14  $\mu\text{m}$  or longer (18–25  $\mu\text{m}$  long in type species), **conus tip tubular**; protractors attached mostly to bulboid vestibulum extension of cephalic framework. Median bulb strongly muscular, round to oval. Basal bulb offset from intestine. Cardia large, rounded. Intestine may extend over rectum into tail. Vulva post-submedian (at 53–67%), lips not modified. Spermathecae axial, round. Ovaries paired. Female tail cylindroid or subclavate, 1.5–3.5 anal body widths long; **terminal cuticle abnormally thickened**, more than one-third of tail length, occasionally ‘cupped’ ventrally (*P. bursifer*); tail cytoplasmic core cylindroid, posteriorly hemispheroid or truncate. Males generally present. Tail with large hyaline terminal portion, enveloped by large simple crenate bursa. Spicules prominently flanged distally. Gubernaculum large, protrusible; proximal end rounded or bent ventrally.

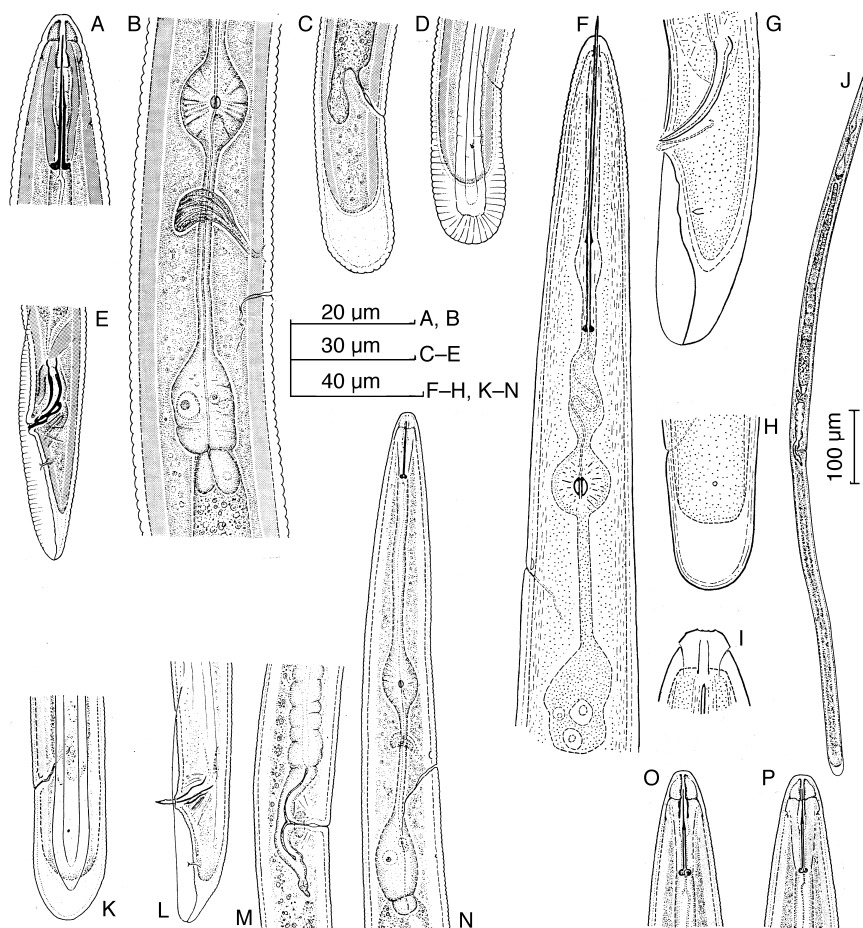
#### Type species

*Paratrophurus loofi* Arias, 1970

#### Other species

- Paratrophurus acristylus* Siddiqi & Siddiqui, 1983  
*P. anomalus* Kleynhans & Heyns, 1983  
*P. bursifer* (Loof, 1960) Siddiqi, 1971  
 syn. *Tylenchorhynchus bursifer* Loof, 1960  
*P. costarricensis* López, 1986  
*P. dissitus* (Colbran, 1969) Siddiqi, 1971  
 syn. *Tylenchorhynchus dissitus* Colbran, 1969  
*P. hungaricus* Andrassy, 1973





**Fig. 107.** A–E. *Paratrophurus loofi* Arias. F–I. *Macrotrophurus arbusticola* Loof. J–P. *Trophurus imperialis* Loof. A, I and O. Head ends of females. B. Posterior region of oesophagus. C, D, H and K. Tail ends of females. E, G and L. Tail ends of males. F and N. Oesophageal regions of females. J. Entire female. M. Vulval region showing postvulval uterine sac. P. Head end of male. (J–P. After Siddiqi (1973): *CIH Descriptions of Plant-parasitic Nematodes*.)

*P. indicans* Kleynhans, 1992

*P. kenanae* Decker & El Amin, 1978

*P. kleyinsi* Castillo, Siddiqi & Gomez-Barcina, 1989

*P. perissus* Kleynhans, 1992

*P. sacchari* Edward & Sharma, 1984

*P. striatus* Castillo, Siddiqi & Gomez-Barcina, 1989

**ETYMOLOGY.** From Greek *para* = beside, near, and *Trophurus*.

The type species was found around roots of wheat in Seville, Spain.

**Genus *Trophurus* Loof, 1956****syn. *Clavaurotylenchus* Caveness, 1958**

(Fig. 107, J–P)

**Diagnosis**

Telotylenchinae. Body 0.5–1.2 mm long, slender ( $a = 25\text{--}58$ ). Cuticular annulation fine, usually not prominent. Lateral field with four incisures, not areolated. Deirids absent. Phasmids distinct, near middle of tail. Cephalic region elevated, continuous, round or truncate, lacking distinct annulation; **no longitudinal indentations of annules** seen in SEM of face view; framework lightly to moderately sclerotized, with elongate stylet guiding tube. **Stylet slender**, 10–22  $\mu\text{m}$  long with solid-appearing tip and small round knobs. Median bulb oval, muscular, behind middle of oesophagus. Basal bulb pyriform, offset from intestine or dorsal gland may slightly extend over intestine; cardia prominent. Vulva at 52–66% of body length, lips not modified. **Ovary single**, outstretched. **Posterior branch represented by a uterine sac, often carrying rudiments of posterior ovary.** Spermatheca with offset lobes. Intestine usually extending over rectum into tail cavity. Female tail cylindroid, subclavate or subconoid with broadly rounded terminus, 1.2–3 anal body widths long; **hyaline terminal cuticle very prominent.** Males present. Spicules slender, about 11–25  $\mu\text{m}$  long. Gubernaculum small, linear, fixed. Bursa large, enveloping tail, terminally indented in type species.

**Type species***Trophurus imperialis* Loof, 1956**Other species***Trophurus deboeri* Kleynhans & Cadet, 1994*T. impar* Ganguly & Khan, 1983 (syn. of *T. longimarginatus* for Rahaman & Sharma, 1998)*T. lomus* Saha, Chawla & Khan, 1974*T. longimarginatus* Román, 1962 (*Trophurus longimarginatus* Singh, 1973 = nomen nudum)*T. marathwadensis* Suryawanshi, 1971*T. minnesotensis* (Caveness, 1958) Caveness, 1959syn. *Clavaurotylenchus minnesotensis* Caveness, 1958*T. pakendorfi* De Waele & Bolton, 1988*T. roigi* Razjivin, O'Relly & Pérez Milian, 1973*T. scognamiglii* Talamé, 1974*T. sculptus* Loof, 1956*T. similis* Khan & Nanjappa, 1971*T. ussuriensis* Eroshenko, 1981*T. vultus* Siddiqi & Lenné, 1990ETYMOLOGY. From Greek *trophoeis* = swollen, and *oura* = tail.

The type species was found in soil from an alfalfa field (*Medicago sativa* L.) at Gronsveld, Limburg province, The Netherlands. *Trophurus* spp. have been reported

from Asia, Europe, Africa and North and South America. Kleynhans & Cadet (1994) gave tabular and dichotomous keys to species of *Trophurus*.

## Subfamily Meiodorinae Siddiqi, 1976

### Diagnosis

Telotylenchidae. Medium-sized (about 1 mm), slender. Lateral fields each with three incisures. Phasmids postanal. **Cephalic region circular or hexagonal**, offset, annulated; framework weakly sclerotized. **Labial disc indistinct**. **Stylet under 40  $\mu\text{m}$  long; conus about as long as shaft**; knobs prominent. Orifice of dorsal oesophageal gland close to stylet base. **Median bulb behind middle of oesophagus**. Postrectal intestinal sac absent; intestinal fasciculi present. Vulva a transverse slit, closed. Vagina without sclerotization. Ovaries paired. Spermathecae round or oval, axial. **Female tail elongate-conoid, pointed, over four anal body widths long, with a large hyaline terminal portion**. Male tail short, less than two body widths long, **enveloped by a trilobed bursa; lateral lobes of bursa large, pointed and directed posteriorly**. Spicules robust, cephalated, arcuate, with or without distal flanges. Gubernaculum well developed, protrusible.

### Type genus

*Meiodorus* Siddiqi, 1976

No other genus.

### Genus *Meiodorus* Siddiqi, 1976

**syn. *Mulveyotus* Anderson & Ebsary, 1982**

(Figs 97, I–P; 104(b), E)

### Diagnosis

Meiodorinae. Straight to ventrally arcuate upon relaxation. **Lateral field with three incisures, areolated**. Cephalic region offset, annulated; **framework lightly sclerotized**; labial disc inconspicuous. **Stylet slender**, 11–26  $\mu\text{m}$  long; conus about half its length; knobs rounded. Median bulb slightly set off from precorpus, with refractive thickenings. Basal bulb pyriform. Vulva with thick, raised labia, closed. **Vagina not sclerotized**. Spermathecae round or oval, axial. Ovaries outstretched. Female tail elongate-conoid to a finely rounded or mucronate tip; hyaline terminal portion about quarter or more of tail length (12–26  $\mu\text{m}$  long and phasmids at 18–22  $\mu\text{m}$  behind anus in type species). Bursa trilobed; lateral lobes of bursa not projecting beyond tail tip. Spicules flanged. Gubernaculum rod-like, protrusible.

### Type species

*Meiodorus hollisi* Siddiqi, 1976

### Other species

*Meiodorus festonatus* Doucet, 1985

*M. hyalacus* (Anderson & Ebsary, 1982) Siddiqi, 1986

syn. *Mulveyotus hyalacus* Anderson & Ebsary, 1982

ETYMOLOGY. From Greek *meion* = smaller, lesser, and *dory* = spear.

The type species was found in rice fallow soil at Klondike, Louisiana, USA.

## Subfamily Macrotrophurinae Fotedar & Handoo, 1978

### Diagnosis

Telotylenchidae. **Cuticle thick, smooth** with annulation discernible only in a short zone behind cephalic region. Lateral field with four smooth incisures, **an irregular row of pores along each of the inner incisures present. Amphidial apertures, distinct, transversely oval, postlabial.** Deirids absent. Cephalic region smooth, rounded, continuous; framework lightly sclerotized; labial disc absent. **Stylet over 80  $\mu\text{m}$  long.** Postcorpus strongly muscular; basal bulb pyriform. Ovaries paired. **Female tail short** (less than two anal body widths long), rounded; terminal cuticle abnormally thickened. Male tail enveloped by a simple smooth bursa.

### Type genus

*Macrotrophurus* Loof, 1958

No other genus.

### Genus *Macrotrophurus* Loof, 1958

(Fig. 107, F–I)

### Diagnosis

Macrotrophurinae. Cuticle thick, annules indistinct. Medium- to large-sized (1–2 mm), slender ( $a = 38\text{--}58$ ). Lateral fields not areolated, each with four incisures. Cephalic framework weakly developed. **Amphidial apertures prominent, at posterior margins of lateral lip areas. Stylet exceedingly long** (90–110  $\mu\text{m}$  in type species), slender; conus more than twice the length of shaft; knobs small, rounded. Orifice of dorsal gland close to stylet base. Precorpus swollen, with convoluted lumen. Median bulb offset from precorpus, with prominent refractive thickenings. Isthmus elongate-slender. Basal bulb elongate, offset from intestine; cardia prominent. Excretory pore just behind hemizonid. Vulva a transverse slit, at 44–50% of body length. Vagina not sclerotized. Spermathecae broadly oval. Ovaries paired, outstretched in opposite directions. Rectum and anus distinct. Postrectal intestinal sac absent. Female tail short (less than two anal body widths long), cylindroid, terminus smoothly rounded, **with abnormally thickened cuticle.** Phasmids anterior to middle of tail. Male tail about two anal body widths long, with thick cuticle at tip. Spicules distally pointed, 29–35  $\mu\text{m}$  long in type species. Gubernaculum large, hooked proximally, recurved distally.

### Type species

*Macrotrophurus arbusticola* Loof, 1958

No other species.

ETYMOLOGY. From Greek *macras* = large, and *Trophurus*.

The type species was found around roots of trees (pear, apple and poplar) in The Netherlands and Switzerland.

### **Subfamily Merliniinae Siddiqi, 1971** (**Merliniinae Siddiqi, 1970 = nomen nudum**)

#### Diagnosis

Telotylenchidae. **Lateral fields each with six incisures. Deirids present** except in *Scutylenchus*. Phasmids usually prominent, on tail. Cephalic region annulated; labial disc indistinct or distinct (*Geocenamus*). Stylet small to very long (11–130  $\mu\text{m}$ ), with distinct basal knobs. Median and basal bulbs well developed. **Vulva small, pore-like, transversely oval or slit-like**, usually with epitygma. Ovaries paired. **Spermathecae two- to four-lobed. Postrectal intestinal sac absent.** Female tail conoid, subcylindroid, cylindroid or subclavate, between two and six anal body widths long; terminal cuticle may occasionally be strongly thickened. Male tail conical, about as long as that of female. Bursa simple, moderately developed, enveloping tail. **Hypoptygma** (a pair of papillae on posterior lip of cloaca) **always present.** **Spicules cylindroid in distal half**, straight to slightly arcuate, **with distal end broadly rounded, notched and devoid of ventro-lateral flanges or vela.** **Gubernaculum simple, trough-like, fixed.**

#### Type genus

*Merlinius* Siddiqi, 1970

#### Other genera

*Amplimerlinius* Siddiqi, 1976  
*Geocenamus* Thorne & Malek, 1968  
*Nagelus* Thorne & Malek, 1968  
*Scutylenchus* Jairajpuri, 1971

#### Key to genera of Merliniinae

1. Body cuticle with longitudinal striae or grooves; deirids absent ..... *Scutylenchus*  
Body cuticle without longitudinal striae or grooves; deirids present ..... 2
2. Cephalic annules broken by radial grooves ..... 3  
Cephalic annules not broken ..... 4
3. Stylet elongate (25–130  $\mu\text{m}$ ), with conus more than 50% of its total length;  
perioral disc well marked, rounded ..... *Geocenamus*  
Stylet not so elongate, with conus less than 50% of its total length; perioral  
disc not marked, rectangular to oval ..... *Merlinius*
4. Cephalic region continuous; female tail cylindrical to subclavate, terminal  
cuticle abnormally thickened ..... *Amplimerlinius*  
Cephalic region slightly offset; female tail tapering, terminal cuticle slightly  
thickened ..... *Nagelus*

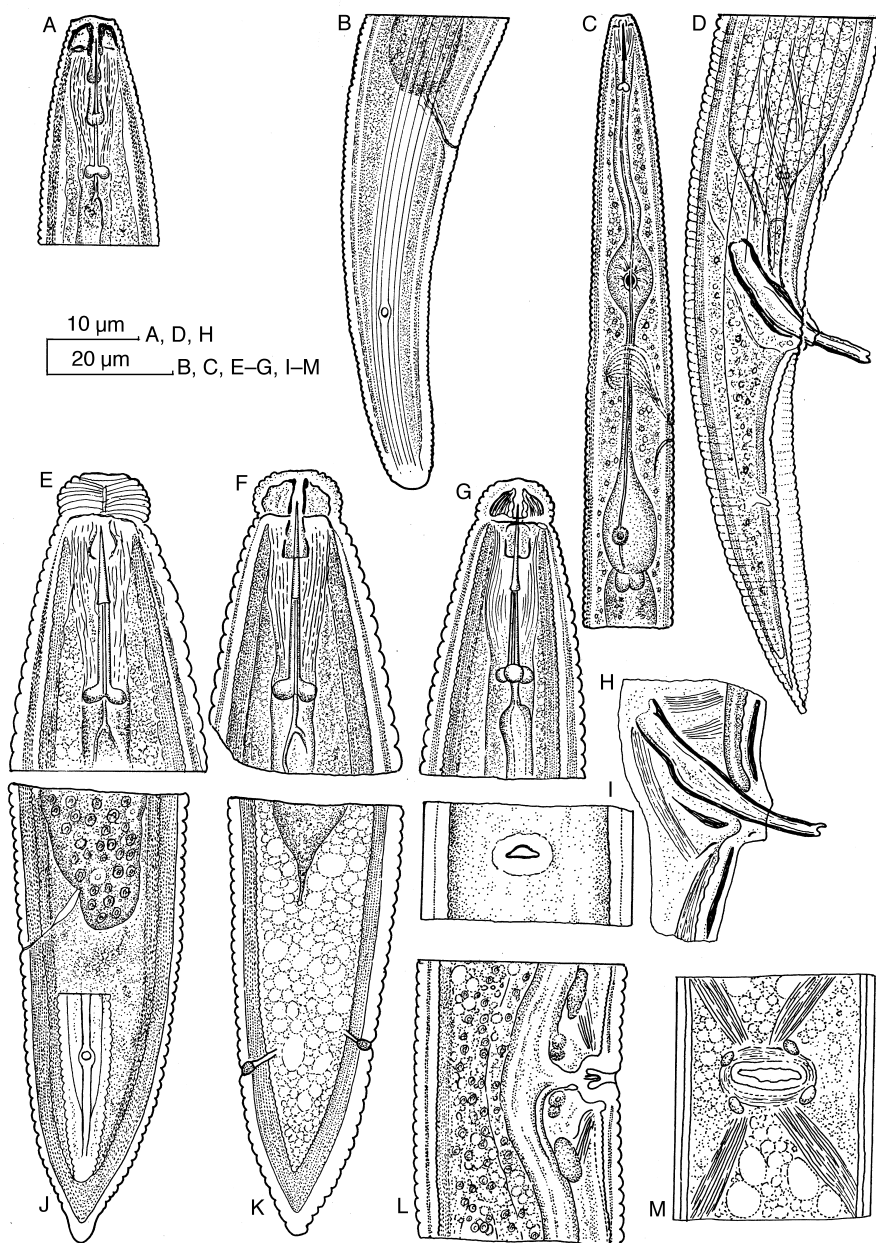
**Genus *Merlinius* Siddiqi, 1970****syn. *Allentylenchus* Khan & Saeed, 1988; syn. n.**

(Fig. 108(a)A–D, (b), C &amp; F)

**Diagnosis**

Merliniinae. Under 1 mm long, straight to arcuate upon relaxation. Body cuticle lacking longitudinal striae or grooves; lateral fields with six incisures, normally not areolated behind oesophageal region. **Deirids distinct, in four-incisure region of lateral field.** Cephalic region continuous or slightly offset, not bulbous; **annules broken by six radial grooves; perioral disc indistinct, hexagonal, not well demarcated from surrounding labial area; submedian sectors wider than lateral sectors bearing amphidial apertures which are not at the border of oral plate but more posterior.** Stylet usually under 20  $\mu\text{m}$  long, with conus half stylet length or shorter. Median bulb at or anterior to middle of oesophagus. **Vulva closed, slit-like;** epiptygma indistinct. Vagina vera in lateral view irregular, not squarish. Female tail conoid to subcylindrical; **terminal cuticle of normal thickness.** Spicules cylindroid, straight to slightly arcuate, tip blunt and notched. Gubernaculum crescent-shaped in lateral view.

**Type species***Merlinius brevidens* (Allen, 1955) Siddiqi, 1970syn. *Tylenchorhynchus brevidens* Allen, 1955*Geocenamus brevidens* (Allen) Brzeski, 1991**Other species***Merlinius acuminatus* Minagawa, 1985syn. *Geocenamus acuminatus* (Minagawa, 1985) Brzeski, 1991*M. adakensis* Bernard, 1984syn. *Geocenamus adakensis* (Bernard) Brzeski, 1991*M. alboranensis* (Tobar-Jiménez, 1970) Tarjan, 1973syn. *Tylenchorhynchus alboranensis* Tobar-Jiménez, 1970*Nagelus alboranensis* (Tobar-Jiménez) Siddiqi, 1986*Geocenamus alboranensis* (Tobar-Jiménez) Brzeski, 1991*M. bavaricus* (Sturhan, 1966) Siddiqi, 1970syn. *Tylenchorhynchus bavaricus* Sturhan, 1966*Geocenamus bavaricus* (Sturhan) Brzeski, 1991*M. bijnorensis* Khan, 1971*M. bilqeesae* Khan & Khan, 1995*M. bogdanovikatjkovi* (Kirjanova, 1941) Siddiqi, 1970syn. *Anguillulina bogdanovikatjkovi* Kirjanova, 1941*Tylenchorhynchus bogdanovikatjkovi* (Kirjanova) Loof, 1959*M. capitonis* Ivanova, 1983syn. *Geocenamus capitonis* (Ivanova) Brzeski, 1991*M. circellus* Anderson & Ebsary, 1982syn. *Geocenamus circellus* (Anderson & Ebsary) Brzeski, 1991*M. communicus* Sultan, Singh & Sakhuja, 1989syn. *Geocenamus communicus* (Sultan, Singh & Sakhuja) Brzeski, 1992



**Fig. 108(a).** A–D. *Merlinius brevidens* (Allen), paratypes. E–M. *Scutylenchus mamillatus* (Tobar Jiménez) from tomato soil in Morocco. D, G and H. Males, remainder females. A, E–G. Head ends. B, D, J and K. Tail ends. C. Oesophageal region. H. Spicular region. I, L and M. Vulval regions.

- M. gatevi* Budurova, 1988  
*M. graminicola* (Kirjanova, 1951) Siddiqi, 1976  
     syn. *Tylenchorhynchus graminicola* Kirjanova, 1951  
         *Allentylenchus graminicola* (Kirjanova) Khan & Saeed, 1988  
*M. indicus* Zarina & Maqbool, 1995  
     syn. *Geocenamus indicus* (Zarina & Maqbool) Brzeski, 1998  
*M. joctus* (Thorne, 1949) Sher, 1974  
     syn. *Tetylenchus joctus* Thorne, 1949  
         *Geocenamus joctus* (Thorne) Brzeski, 1991  
*M. loofi* Siddiqi, 1979  
     syn. *Geocenamus loofi* (Siddiqi) Brzeski, 1991  
*M. microdorus* (Geraert, 1966) Siddiqi, 1970  
     syn. *Tylenchorhynchus microdorus* Geraert, 1966  
         *Geocenamus microdorus* (Geraert) Brzeski, 1991  
*M. mollicephalus* Eroshenko & Volkova, 1988  
     syn. *Geocenamus mollicephalus* (Eroshenko & Volkova) Brzeski, 1998  
*M. montanus* Maqbool & Shahina, 1987  
     syn. *Geocenamus montanus* (Maqbool & Shahina) Brzeski, 1992  
*M. nanus* (Allen, 1955) Siddiqi, 1970  
     syn. *Tylenchorhynchus nanus* Allen, 1955  
         *Geocenamus nanus* (Allen) Brzeski, 1991  
*M. niazae* Maqbool, Fatima & Hashmi, 1983  
     syn. *Geocenamus niazae* (Maqbool et al.) Brzeski, 1991  
*M. nothus* (Allen, 1955) Siddiqi, 1970  
     syn. *Tylenchorhynchus nothus* Allen, 1955  
         *Geocenamus nothus* (Allen) Brzeski, 1991  
         *Tylenchorhynchus undyferrus* Haque, 1967  
         *Merlinius undyferrus* (Haque) Siddiqi, 1970  
         *Merlinius paramonovi* Volkova, 1972  
         *Merlinius nizamii* Luqman & Khan, 1986  
         *Merlinius bulgaricus* Budurova, 1988  
         *Merlinius semicircularis* Lüth, 1984  
         *Geocenamus semicircularis* (Lüth) Brzeski, 1991  
*M. pistaciae* Fatema & Farooq, 1992  
*M. planitierus* Eroshenko, 1984  
     syn. *Geocenamus planitierus* (Eroshenko) Brzeski, 1991  
*M. plerorbus* Anderson & Ebsary, 1982  
     syn. *Geocenamus plerorbus* (Anderson & Ebsary) Brzeski, 1991  
*M. processus* Siddiqi, 1979  
     syn. *Geocenamus processus* (Siddiqi) Brzeski, 1991  
*M. productus* (Thorne, 1949) Sher, 1974  
     syn. *Tetylenchus productus* Thorne, 1949  
         *Geocenamus productus* (Thorne) Brzeski, 1991  
*M. pseudobavaricus* Saltukoglu, Geraert & Coomans, 1976  
     syn. *Geocenamus pseudobavaricus* (Saltukoglu et al.) Brzeski, 1991  
*M. pyri* Fatema & Farooq, 1992  
*M. tetylus* Anderson & Ebsary, 1982



- syn. *Geocenamus tetylus* (Anderson & Ebsary) Brzeski, 1991  
*M. tortilis* Kazachenko, 1980  
 syn. *Geocenamus tortilis* (Kazachenko) Brzeski, 1991

### Species inquirendae

- Merlinius salechardicus* Nesterov, 1985  
*Merlinius kirjanovae* (Karapetjan) Eroshenko & Volkova, 1987  
 syn. *Tylenchorhynchus kirjanovae* Karapetjan, 1979  
*Pathotylenchus kirjanovae* (Karapetjan) in Ebsary, 1991

ETYMOLOGY. Patronym honouring Merlin W. Allen.

The type species was described from grass soil in Strawberry Canyon, University of California Campus at Berkeley, California, USA.

### Genus *Scutylenchus* Jairajpuri, 1971

(Figs 8(c), D; 108(a), E–M, (b), D)

#### Diagnosis

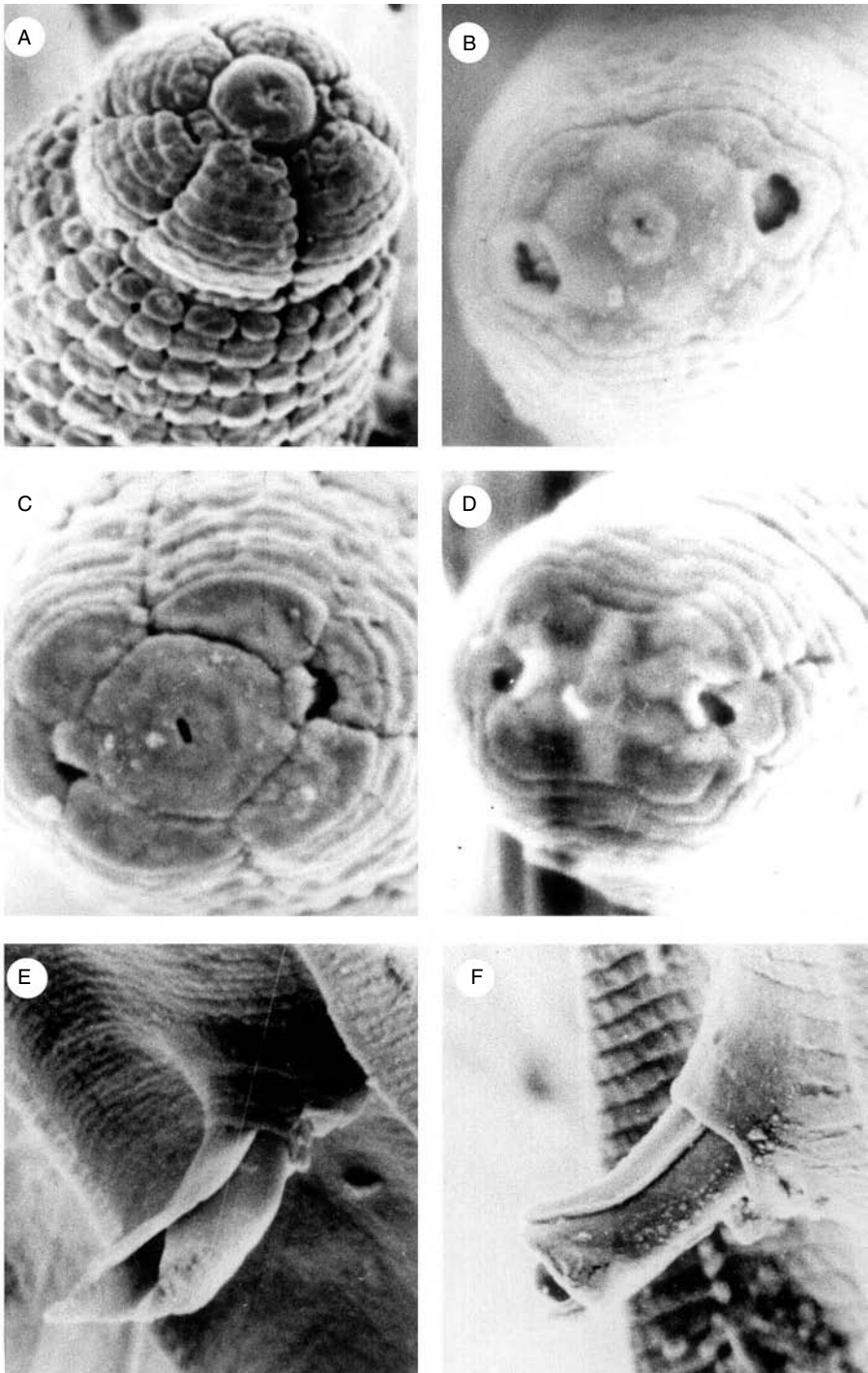
Merliniinae. Small to medium-sized (0.5–1.5 mm), arcuate to curved when relaxed. **Body cuticle marked by longitudinal striae or grooves. Deirids absent. Cephalic region offset, with six radial grooves** and moderate sclerotization; labial disc inconspicuous, four-lobed. Median bulb near middle of oesophagus or more anterior. Vulva in a cavity or depression, with epiptygma. **Vagina vera squarish in lateral view.** Female tail conoid to subcylindrical with rounded tip; terminal tail cuticle not abnormally thickened; phasmids conspicuous. Spicules rather slender; gubernaculum crescent-shaped in lateral view.

#### Type species

- Scutylenchus mamillatus* (Tobar-Jiménez, 1966) Jairajpuri, 1971  
 syn. *Tylenchorhynchus mamillatus* Tobar-Jiménez, 1966  
*Merlinius mamillatus* (Tobar-Jiménez) Anderson, 1977  
*Geocenamus mamillatus* (Tobar-Jiménez) Brzeski, 1991

#### Other species

- Scutylenchus baluchiensis* Maqbool, Ghazala, Fatima & Qasim, 1985  
 syn. *Geocenamus baluchiensis* (Maqbool *et al.*) Brzeski, 1991  
*S. boghiae* (Choi & Geraert, 1994) comb. n.  
 syn. *Geocenamus boghiae* Choi & Geraert, 1994  
*S. brevicaudatus* Peng & Hunt, 1995  
 syn. *Geocenamus brevicaudatus* (Peng & Hunt) Brzeski, 1998  
*S. hexincisus* (Jairajpuri & Baqri, 1968) Siddiqi, 1979  
 syn. *Tylenchorhynchus hexincisus* Jairajpuri & Baqri, 1968  
*Merlinius hexincisus* (Jairajpuri & Baqri) Siddiqi, 1970  
*Geocenamus hexincisus* (Jairajpuri & Baqri) Brzeski, 1991  
*S. koreanus* (Choi & Geraert, 1971) Siddiqi, 1979  
 syn. *Merlinius koreanus* Choi & Geraert, 1971  
*Geocenamus koreanus* (Choi & Geraert) Brzeski, 1991



**Fig. 108(b).** Scanning electron micrographs. A–D. Female heads. E and F. Protruded spicules. A. *Geocenamus longus*. B. *Nagelus aberrans* Thorne & Malek. C and F. *Merlinius microdorus*. D. *Scutylenchus quadrifer* E. *Bitylenchus dubius*. Courtesy IACR-Rothamsted, Harpenden, UK.

- S. laminatus* (Wu, 1969) Anderson & Ebsary, 1982  
syn. *Tylenchorhynchus laminatus* Wu, 1969  
*Merlinius laminatus* (Wu) Siddiqi, 1970  
*Scutylenchus laminatus* (Wu) Siddiqi, 1986  
*Geocenamus laminatus* (Wu) Brzeski, 1991
- S. lenorus* (Brown, 1956) Siddiqi, 1979  
syn. *Tylenchorhynchus lenorus* Brown, 1956  
*Merlinius lenorus* (Brown) Siddiqi, 1970  
*Geocenamus lenorus* (Brown) Brzeski, 1991
- S. myungsugae* (Choi & Geraert, 1994) comb. n.  
syn. *Geocenamus myungsugae* Choi & Geraert, 1994
- S. paniculoides* (Vovlas & Esser, 1990) comb. n.  
syn. *Merlinius paniculoides* Vovlas & Esser, 1990
- S. quadrifer* (Andrássy, 1954) Siddiqi, 1979  
syn. *Tylenchorhynchus quadrifer* Andrásy, 1954  
*Merlinius quadrifer* (Andrássy) Siddiqi, 1970  
*Geocenamus quadrifer* (Andrássy) Brzeski, 1991  
*Tylenchorhynchus ornatus* Allen, 1955  
*Merlinius ornatus* (Allen) Siddiqi, 1970  
*Scutylenchus ornatus* (Allen) Siddiqi, 1986
- S. rugosus* (Siddiqi, 1963) Siddiqi, 1979  
syn. *Tylenchorhynchus rugosus* Siddiqi, 1963  
*Merlinius rugosus* (Siddiqi) Siddiqi, 1970  
*Geocenamus rugosus* (Andrássy) Brzeski, 1991  
*Tylenchorhynchus cylindricaudatus* Ivanova, 1968  
*Scutylenchus cylindricaudatus* (Ivanova) Siddiqi, 1979  
*Merlinius cylindricaudatus* (Ivanova) Siddiqi, 1970  
*Scutylenchus apricus* Andrásy, 1980  
*Merlinius apricus* (Andrássy) Fortuner & Luc, 1987  
*Scutylenchus quettensis* Maqbool, Ghazala & Fatima, 1984  
*Merlinius quettensis* (Maqbool *et al.*) Fortuner & Luc, 1987  
*Geocenamus quettensis* (Maqbool *et al.*) Brzeski, 1991  
*Scutylenchus fici* Farooq & Fatema, 1994  
*Geocenamus fici* (Farooq & Fatema) Brzeski, 1998
- S. siddiqii* (Mulk, 1978) Skwiercz, 1984  
syn. *Merlinius siddiqii* Mulk, 1978  
*Geocenamus siddiqii* (Mulk) Brzeski, 1991
- S. sobolevi* (Mukhina, 1970) Siddiqi, 1979  
syn. *Tylenchorhynchus sobolevi* Mukhina, 1970  
*Merlinius sobolevi* (Mukhina) Tarjan, 1973  
*Geocenamus sobolevi* (Mukhina) Brzeski, 1991
- S. sphaerocephalus* Ivanova, 1982  
syn. *Merlinius sphaerocephalus* (Ivanova) Fortuner & Luc, 1987  
*Geocenamus sphaerocephalus* (Ivanova) Brzeski, 1991
- S. stegus* (Thorne & Malek, 1968) Siddiqi, 1979  
syn. *Tylenchorhynchus stegus* Thorne & Malek, 1968  
*Merlinius stegus* (Thorne & Malek) Siddiqi, 1970  
*Geocenamus stegus* (Thorne & Malek) Brzeski, 1991

- S. tartuensis* (Krall, 1959) Siddiqi, 1979  
 syn. *Tylenchorhynchus tartuensis* Krall, 1959  
*Merlinius tartuensis* (Krall) Siddiqi, 1970  
*Geocenamus tartuensis* (Krall) Brzeski, 1991
- S. tessellatus* (Goodey, 1952) Siddiqi, 1979  
 syn. *Tylenchorhynchus tessellatus* Goodey, 1952  
*Merlinius tessellatus* (Goodey) Siddiqi, 1970  
*Geocenamus tessellatus* (Goodey) Brzeski, 1991
- S. thomasi* Skwierz, 1984  
 syn. *Merlinius thomasi* (Skwierz) Fortuner & Luc, 1987  
*Geocenamus thomasi* (Skwierz) Brzeski, 1991
- S. tumensis* Skwierz, 1984  
 syn. *Merlinius tumensis* (Skwierz) Fortuner & Luc, 1987  
*Geocenamus tumensis* (Skwierz) Brzeski, 1991
- S. variabilis* Ivanova & Shagalina, 1983  
 syn. *Merlinius variabilis* (Ivanova & Shagalina) Fortuner & Luc, 1987  
*Geocenamus variabilis* (Ivanova & Shagalina) Brzeski, 1991

ETYMOLOGY. From *scutellum* = enlarged phasmid, and *Tylenchus*.

The type species was found in sandy soil around roots of potato (*Solanum tuberosum* L.) in Cadiz, Spain.

### **Genus *Geocenamus* Thorne & Malek, 1968**

syn. *Hexadorus* Ivanova & Shagalina, 1983

*Pathotylenchus* Eroshenko & Volkova, 1987

(Figs 108(b), A; 109, A–E; 110, M–R)

### **Diagnosis**

Merliniinae. Medium-sized (about 1 mm or longer), straight to arcuate. Annules in anterior region may be marked by fine longitudinal indentations which do not form longitudinal lines. Lateral fields areolated on tail. Deirids absent. **Cephalic region offset, bulbous, with six radial grooves and a conspicuous, offset, rounded oral disc which is well demarcated from surrounding lip areas, which are distinct, lateral lip areas not distinctly smaller than submedians. Stylet slender, 25–130  $\mu$ m long, with conus markedly longer than shaft** and, in type species, with anterior half solid-appearing; knobs small rounded. Stylet guiding tube elongate-slender. Vulva closed or open; epitygma may be present, anterior lip may extend over vulva. Vagina vera squarish in lateral view. Female tail straight, elongate-conoid to subcylindroid, with rounded tip. Spicules rather slender, slightly arcuate, bluntly rounded and notched at tip. Gubernaculum crescent-shaped in lateral view.

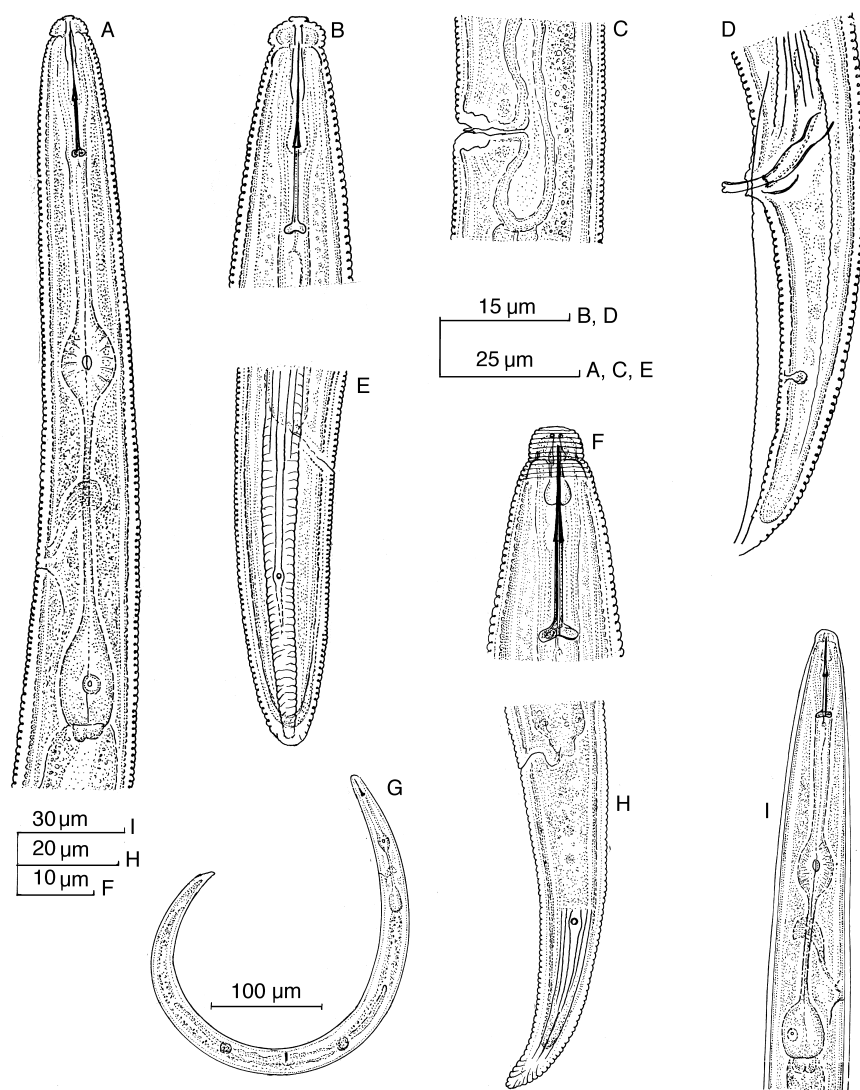
### **Type species**

*Geocenamus tenuidens* Thorne & Malek, 1968

syn. *Tylenchorhynchus polonicus* Szczygieł, 1970

*Merlinius polonicus* (Szczygieł) Tarjan, 1973

*Geocenamus polonicus* (Szczygieł) Sturhan, 1981



**Fig. 109.** A–E. *Geocenamus tenuidens* Thorne & Malek, paratypes. F–I. *Nagehus* spp. G. *Nagehus camelliae* (Kheiri), holotype female in death position. F and H. *Nagehus leptus* (Thorne), paratypes of *N. aberrans* Thorne & Malek (= *N. leptus*). A and I. Oesophageal regions. B and F. Head ends of females. C. Vulval region. D. Tail end of male. E and H. Tail ends of females. (A–I. After Siddiqi (1979c), courtesy Systematic Parasitology.)

### Other species

*Geocenamus arcticus* (Mulvey, 1969) Tarjan, 1973 (syn. of *G. tenuidens* for Brzeski, 1998)

syn. *Tylenchorhynchus arcticus* Mulvey, 1969

*Merlinius arcticus* (Mulvey) Sturhan, 1981

- G. arealoferus* (Razjivin, 1971) Fortuner & Luc, 1987  
 syn. *Morulaimus arealoferus* Razjivin, 1971  
     *Hexadorus arealoferus* (Razjivin) Ivanova & Shagalina, 1983  
     *Geocenamus arealoferus* (Razjivin) Brzeski, 1991
- G. deserticola* (Ivanova & Shagalina, 1983) Fortuner & Luc, 1987  
 syn. *Hexadorus deserticola* Ivanova & Shagalina, 1983
- G. khashanicus* Volkova, 1995
- G. kirjanovae* (Sagitov, 1973) Fortuner & Luc, 1987  
 syn. *Dolichodorus kirjanovae* Sagitov, 1973  
     *Merlinius kirjanovae* (Sagitov) Loof & Sharma, 1975  
     *Nagelus kirjanovae* (Sagitov) Siddiqi, 1979  
     *Hexadorus kirjanovae* (Sagitov) Siddiqi, 1986  
     *Pathotylenchus kirjanovae* (Sagitov) Eroshenko & Volkova, 1987
- Geocenamus longus* (Wu, 1969) Tarjan, 1973  
 syn. *Tylenchorhynchus longus* Wu, 1969  
     *Scutylenchus longus* (Wu) Skwiercz, 1984  
     *Merlinius longus* (Wu) Sturhan, 1981  
     *Pathotylenchus longus* (Wu) Eroshenko & Volkova, 1987  
     *Geocenamus longus* (Wu) Brzeski, 1991
- G. nurserus* (Eroshenko & Volkova) Fortuner & Luc, 1990 (Brzeski (1991) also proposed this combination)  
 syn. *Pathotylenchus nurserus* Eroshenko & Volkova, 1987  
     *Merlinius nurserus* (Eroshenko & Volkova, 1987) Fortuner & Luc, 1990
- G. patternus* Eroshenko & Volkova, 1987
- G. squamatus* Eroshenko & Volkova, 1988
- G. superbis* (Allen, 1955) Fortuner & Luc, 1990  
 syn. *Tylenchorhynchus superbis* Allen, 1955  
     *Merlinius superbis* (Allen) Siddiqi, 1970  
     *Merlinius superbis* (Allen) Eroshenko & Volkova, 1987  
     *Nagelus superbis* (Allen) Siddiqi, 1979  
     *Pathotylenchus superbis* (Allen) Eroshenko & Volkova, 1987  
     *Geocenamus superbis* (Allen) Brzeski, 1991
- G. tokobaevi* (Sultanalieva, 1983) Fortuner & Luc, 1987  
 syn. *Morulaimus tokobaevi* Sultanalieva, 1983  
     *Hexadorus tokobaevi* (Sultanalieva) Siddiqi, 1986
- G. uralensis* Baydulova, 1983

## Notes

Fortuner & Luc (1987) and Maggenti *et al.* (1988) recognized *Geocenamus* as a valid genus under the subfamily Belonolaiminae, considering *Hexadorus* Ivanova & Shagalina, 1983 as its junior synonym. The related genus *Merlinius* was assigned to Telotylenchinae. Fortuner & Luc (1987) stated: '*Geocenamus* was originally proposed in Telotylenchinae, and said by Siddiqi (1979) to be related to *Merlinius*. Like *Sauertylenchus*, its bulbous labial region, round labial disc, and sometimes elongate stylet are derived characters that prompted us to move this small genus to Belonolaiminae.... *Geocenamus* differs from *Sauertylenchus* by the smaller body length and the shape of male spicules. The six lines in lateral fields provide an easy

way to differentiate the two genera.' However, both *Geocenamus* and *Merlinius* belong in the subfamily Merliniinae, particularly due to the characters of the lateral field, spicule, gubernaculum and hypopygium.

*Hexadorus* was assigned to the subfamily Belonolaiminae and differentiated from the genera of this subfamily by the characters of the lateral field having six incisures and the cephalic region being six-lobed and having a small rounded labial disc. On studying the descriptions and figures of the type species and other nominal species included in the genus by Ivanova & Shagalina, namely, *H. arealoferus*, it becomes evident that the overlap by the dorsal oesophageal gland is only slight. Moreover, the six incisures in the lateral field, the offset and lobed spermathecae and the male spicule and gubernaculum characters leave no doubt that *Hexadorus* is a member of the Merliniinae. It is similar to *Geocenamus* in having a six-lobed cephalic region and an elongate-slender stylet and also to long-stylet species of *Nagelus* (*N. affinis*, *N. alpinus*, *N. conicus*, *N. grandis*, *N. hexagrammus*, *N. lineatus*, *N. macrodens*, *N. superbus*), which have been shown to have six longitudinal striae dividing the cephalic region into six lobes, and thus not to fit properly in *Nagelus* (Powers *et al.*, 1983). These species can be accommodated in *Geocenamus* on the basis of an offset cephalic framework, distinct round to oval labial disc and elongate stylet. Powers *et al.* (1983) have returned them to *Merlinius* (also see Brzeski, 1991a). *Hexadorus* is here considered as a junior synonym of *Geocenamus*, as proposed by Fortuner & Luc (1987).

Brzeski (1991a) synonymized *Merlinius* with *Geocenamus* and gave a key to species. Volkova (1995) did not accept Brzeski's proposal of synonymizing *Merlinius*, *Hexadorus*, *Pathotylenchus* and *Scutylenchus* with *Geocenamus*, and accepted *Geocenamus* with only five species, three of which were from the Russian Far East (*G. tenuidens*, *G. patterns* and *G. squamatus*). *Geocenamus* is recognized here to accommodate long-stylet Merliniinae with a bulbous, six-sectored cephalic region bearing a well-marked, rounded, perioral disc. *Pathotylenchus* was considered a junior synonym of *Geocenamus* by Fortuner & Luc (1990).

ETYMOLOGY. From the geographical centre of North America (Geo-ce-n-am-us) i.e. North Dakota, the type locality of the type species.

The type species was collected from prairie sod near Rugby, North Dakota, USA. The type species of *Hexadorus*, *H. deserticola*, was found in the rhizosphere of *Haloxylon persicum* in the desert of Kara-kum, southern Tadzhikistan. It also occurs in central Asian deserts.

### Genus *Nagelus* Thorne & Malek, 1968

(Figs 108(b), B; 109, F–I)

#### Diagnosis

Merliniinae. Medium-sized (about 1 mm or longer), arcuate to strongly curved. Cephalic region elevated, slightly offset by expansion; annules not broken by radial grooves or indentations; face view broadly oval; perioral disc inconspicuous, partially or completely fused with first lip annule; amphidial apertures within limits of first annule; sclerotization moderate to strong. **Deirids conspicuous, in six-incisure**

region of lateral field. Stylet robust, about 20–40  $\mu\text{m}$  long; conus tubular until tip, about as long as shaft; knobs posteriorly sloping. Median bulb usually behind middle of oesophagus. Basal bulb large, saccate. **Vulva round to transversely oval**, usually covered by epiptygma. Vagina vera in lateral view not appearing squarish. **Female tail elongate-conoid to subcylindrical, contour usually irregular, slightly arcuate; terminus with a distinct hyaline region.** Spicules robust, almost straight. Gubernaculum in lateral view appearing to have a thickened rounded proximal region, a median concavity and distal end drawn out and directed posteriorly.

#### Type species

*Nagelus aberrans* Thorne & Malek, 1968

#### Present status

*Nagelus leptus* (Allen, 1955) Siddiqi, 1979  
 syn. *Tylenchorhynchus leptus* Allen, 1955  
*Merlinius leptus* (Allen) Siddiqi, 1970  
*Nagelus aberrans* Thorne & Malek, 1968  
*Merlinius abalosi* Doucet, 1978  
*Nagelus abalosi* (Doucet) Doucet, 1980  
*Merlinius virginalis* Doucet, 1978  
*Nagelus virginalis* (Doucet) Doucet, 1980  
*Nagelus saifulmulukensis* Maqbool & Shahina, 1987

#### Other species

*Nagelus affinis* (Allen, 1955) Siddiqi, 1979  
 syn. *Tylenchorhynchus affinis* Allen, 1955  
*Merlinius affinis* (Allen) Siddiqi, 1970  
*Geocenamus affinis* (Allen) Brzeski, 1991  
*N. alpinus* Doucet & Luc, 1981 (syn. of *N. obscurus* for Brzeski, 1997)  
*N. alpinus* (Allen, 1955) Siddiqi, 1979  
 syn. *Tylenchorhynchus alpinus* Allen, 1955  
*Merlinius alpinus* (Allen) Siddiqi, 1970  
*Geocenamus alpinus* (Allen) Brzeski, 1991  
*N. arenosus* Ivanova & Shagalina, 1983  
 syn. *Geocenamus arenosus* (Ivanova & Shagalina) Brzeski, 1991  
*N. borealis* Powers, Baldwin & Bell, 1983  
*N. camelliae* (Kheiri, 1972) Siddiqi, 1979 (syn. of *N. obscurus* for Brzeski, 1997)  
 syn. *Merlinius camelliae* Kheiri, 1972  
*N. conicus* (Allen, 1955) Siddiqi, 1979  
 syn. *Tylenchorhynchus conicus* Allen, 1955  
*Merlinius conicus* (Allen) Siddiqi, 1970  
*Geocenamus conicus* (Allen) Brzeski, 1991  
*N. curiosus* (Wilski, 1965) Siddiqi, 1986  
 syn. *Tetylenchus curiosus* Wilski, 1965  
*Merlinius curiosus* (Wilski) Sher, 1974  
*Geocenamus curiosus* (Wilski) Brzeski, 1991  
*N. djungaricus* (Razjivin, 1974) Kapoor, 1983



- syn. *Tylenchorhynchus djungaricus* Razjivin, 1974  
    *Merlinius djungaricus* (Razjivin) Mahajan & Bello, 1986  
    *Geocenamus djungaricus* (Razjivin) Brzeski, 1992
- N. elongatus* Ivanova & Shagalina, 1983  
    syn. *Geocenamus elongatus* (Ivanova & Shagalina) Brzeski, 1991
- N. exactus* Volkova, 1993
- N. falcatus* (Eroshenko, 1981) Siddiqi, 1986  
    syn. *Merlinius falcatus* Eroshenko, 1981  
    *Geocenamus falcatus* (Eroshenko) Brzeski, 1991
- N. gaudialis* (Izatullaeva, 1967) Siddiqi, 1986  
    syn. *Tylenchorhynchus gaudialis* Izatullaeva, 1967  
    *Merlinius gaudialis* (Izatullaeva) Tarjan, 1973  
    *Geocenamus gaudialis* (Izatullaeva) Brzeski, 1991  
    *Tylenchorhynchus tatrensis* Sabova, 1967  
    *Merlinius tatrensis* (Sabova) Tarjan, 1973  
    *Nagelus tatrensis* (Sabova, 1967) Siddiqi, 1986
- N. gerriae* Khan & Singh, 1999
- N. grandis* (Allen, 1955) Siddiqi, 1979  
    syn. *Tylenchorhynchus grandis* Allen, 1955  
    *Merlinius grandis* (Allen) Siddiqi, 1970  
    *Geocenamus grandis* (Allen) Brzeski, 1991
- N. hexagrammus* (Sturhan, 1966) Siddiqi, 1979  
    syn. *Tylenchorhynchus hexagrammus* Sturhan, 1966  
    *Merlinius hexagrammus* (Sturhan) Siddiqi, 1970  
    *Geocenamus hexagrammus* (Sturhan) Brzeski, 1991  
    *Tylenchorhynchus berberidis* Sethi & Swarup, 1968  
    *Merlinius berberidis* (Sethi & Swarup) Siddiqi, 1970  
    *Nagelus berberidis* (Sethi & Swarup) Siddiqi, 1986  
    *Nagelus ivanovae* Baydulova, 1983
- N. jamalensis* (Nesterov, 1973) Siddiqi, 1979  
    syn. *Tylenchorhynchus jamalensis* Nesterov, 1973  
    *Merlinius jamalensis* (Nesterov) Hooper, 1978  
    *Merlinius jamalensis* (Nesterov) Mulk, 1978
- N. lineatus* (Allen, 1955) Siddiqi, 1979  
    syn. *Tylenchorhynchus lineatus* Allen, 1955  
    *Merlinius lineatus* (Allen) Siddiqi, 1970  
    *Geocenamus lineatus* (Allen) Brzeski, 1991
- N. macrodens* (Allen, 1955) Siddiqi, 1979  
    syn. *Tylenchorhynchus macrodens* Allen, 1955  
    *Merlinius macrodens* (Allen) Siddiqi, 1970  
    *Geocenamus macrodens* (Allen) Brzeski, 1991
- N. macrophasmidus* (Khan & Darekar, 1979) Siddiqi, 1986  
    syn. *Merlinius macrophasmidus* Khan & Darekar, 1979  
    *Geocenamus macrophasmidus* (Khan & Darekar) Brzeski, 1991
- N. neohexagrammus* (Ivanova, 1978) Kapoor, 1983  
    syn. *Merlinius neohexagrammus* Ivanova, 1978  
    *Geocenamus neohexagrammus* (Ivanova) Brzeski, 1991

- N. obscurus* (Allen, 1955) Powers, Baldwin & Bell, 1983  
 syn. *Tylenchorhynchus obscurus* Allen, 1955  
*Merlinius obscurus* (Allen) Siddiqi, 1970  
*Tylenchorhynchus goodeyi* Marinari, 1962  
*Quinisulcius goodeyi* (Marinari) Siddiqi, 1971  
*Nagelus goodeyi* (Marinari) Siddiqi, 1986
- N. parobscurus* (Mulvey, 1969) Siddiqi, 1986  
 syn. *Tylenchorhynchus parobscurus* Mulvey, 1969  
*Merlinius parobscurus* (Mulvey) Kheiri, 1972  
*Merlinius parobscurus* (Mulvey) Tarjan, 1973  
*Geocenamus parobscurus* (Mulvey) Brzeski, 1991
- N. sobaekensis* (Choi & Geraert, 1994) comb. n.  
 syn. *Geocenamus sobaekensis* Choi & Geraert, 1994
- N. varians* (Thorne & Malek, 1968) Siddiqi, 1986  
 syn. *Tylenchorhynchus varians* Thorne & Malek, 1968  
*Merlinius varians* (Thorne & Malek) Siddiqi, 1970  
*Merlinius varians* (Thorne & Malek) Khan & Saeed, 1988  
*Geocenamus varians* (Thorne & Malek) Brzeski, 1991  
*Scutylenchus varians* (Thorne & Malek) Khan & Saeed, 1988

#### Note

Some species of *Nagelus* having radial grooves in cephalic region were returned to *Merlinius* by Powers *et al.* (1983) (see remarks under *Geocenamus*).

ETYMOLOGY. Patronym honouring C.M. Nagel (South Dakota State University, USA).

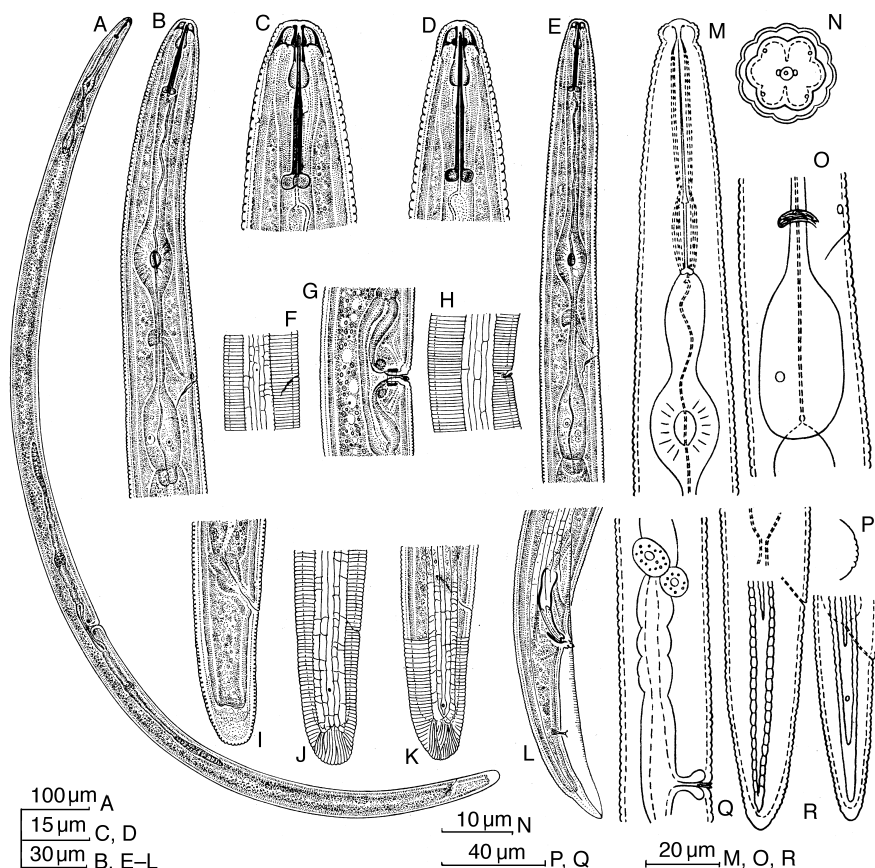
The type species, *N. aberrans*, was described from specimens obtained from hillside thicket, 6 miles west of Wilmot, South Dakota, from primary sod, Granville, North Dakota and from meadow near Sylvan Lake, Black Hills, South Dakota.

#### Genus *Amplimerlinius* Siddiqi, 1976

(Figs 11, E & F; 108(b), F; 110, A–L)

#### Diagnosis

Merliniinae. Medium- to large-sized (1–2 mm), arcuate to strongly curved upon relaxation. Cuticle with prominent, smooth annules. Lateral fields generally with areolations. **Deirids distinct, in six-incisure region of lateral field. Cephalic region continuous with body contour**, minutely but distinctly annulated, **annules not broken by radial grooves or indentations**; face view rounded; framework heavily sclerotized, inner margins forming a large bulboid stylet guide; perioral disc indistinct. **Stylet robust**, 21–42  $\mu\text{m}$  long, with conus tubular up to tip; knobs large. Median bulb well developed, at or behind middle of oesophagus. Vulva open, in a small cavity, with epiptygma. Vagina not sclerotized. **Female tail cylindrical**, occasionally subclavate, with hemispherical, annulated terminus; **cuticle abnormally thickened at tip**. Spicules robust, slightly arcuate, blunt and notched at tip. Gubernaculum trough-shaped in lateral view.



**Fig. 110.** A–L. *Amplimerlinius amplus* Siddiqi. M–R. *Hexadorus* (= *Geocenamus*) *deserticola* Ivanova & Shagalina. A. Female. B. Oesophageal region of male. C and D. Head end of female and male, respectively. E and M. Anterior regions. F, H and P. Lateral fields. G and Q. Vulval regions. I–K and R. Tail ends of females. L. Tail end of male. N. *En face* view. O. Basal oesophageal bulb. (A–L. After Siddiqi (1976), courtesy *Nematologica*. M–R. After Ivanova & Shagalina (1983).)

### Type species

*Amplimerlinius amplus* Siddiqi, 1976

### Other species

*Amplimerlinius clavicaudatus* (Choi & Geraert, 1975) Siddiqi, 1976

syn. *Merlinius clavicaudatus* Choi & Geraert, 1975

*A. ekbali* Khan & Singh, 1999

*A. globigerus* Siddiqi, 1979

*A. hornensis* Bello, Mahajan & Zancada, 1987

*A. icarus* (Wallace & Greet, 1964) Siddiqi, 1976

- syn. *Tylenchorhynchus icarus* Wallace & Greet, 1964  
*Merlinius icarus* (Wallace & Greet) Siddiqi, 1970  
*A. intermedius* (Bravo, 1976) Siddiqi, 1976  
 syn. *Merlinius intermedius* Bravo, 1976  
*A. longicauda* Castillo, Siddiqi & Gómez-Barcina, 1990  
*A. macrurus* (Goodey, 1932) Siddiqi, 1976  
 syn. *Anguillulina macrura* Goodey, 1932  
*Tylenchorhynchus macrurus* (Goodey) Filipjev, 1936  
*Merlinius macrurus* (Goodey) Siddiqi, 1970 in Tarjan, 1973  
*Merlinius caroli* Fortuner, 1985 (was a nom. nov.)  
*Amplimerlinius caroli* (Fortuner, 1985) Siddiqi, 1986 (syn. *Aphelenchus dubius* Steiner, 1914 in Goodey, 1932)  
*Aphelenchus dubius* Steiner, 1914 (was a secondary homonym rejected before 1961, hence not an available name)  
*Merlinius dubius* (Steiner) Siddiqi, 1970  
*Amplimerlinius dubius* (Steiner) Siddiqi & Klingler, 1980  
*A. magnistylus* Castillo, Gómez Barcina, Vovlas & Navas, 1991  
*A. nectolineatus* Siddiqi, 1976  
*A. omentelus* Kleynhans & Heyns, 1983  
*A. paraglobigerus* Castillo, Siddiqi & Gómez Barcina, 1990  
*A. parvati* Zarina & Maqbool, 1990  
*A. quercinus* Mahajan, 1996  
*A. siddiqii* Mancini, Cotroneo & Moretti, 1982  
*A. sikkimensis* Shaw & Khan, 1992  
*A. socialis* (Andrássy, 1962) Siddiqi, 1976  
 syn. *Tylenchorhynchus socialis* Andrásy, 1962  
*Merlinius socialis* (Andrássy) Siddiqi, 1970  
*A. umbonatus* Ivanova, 1982  
*A. viciae* (Saltukoglu, 1973) Siddiqi, 1976  
 syn. *Merlinius viciae* Saltukoglu, 1973

ETYMOLOGY. From Latin *amplus* = large, and *Merlinius*.

The type species was described from specimens collected from soil around roots of olive trees, Canha, Portugal. A key to species is given by Shaw & Khan (1992).

### Genus *Tetylenchus* Filipjev, 1936 (= genus *dubium*)

*Tetylenchus* Filipjev, 1936 is based on *Tylenchus tenuis* Micoletzky as its type species. *Tetylenchus tenuis* (Micoletzky) Filipjev, 1936 is not adequately described. On the available information it is not possible to assign it to any genus with certainty. The holotype in the Zoological Museum of the Humboldt University, Berlin, is the only existing type-material. It has been studied and redescribed by Sher (1974) and Siddiqi (1979) who concluded that the species should be considered species dubia. Sher (1974) believed it to be related to *Merlinius*, but Siddiqi (1979) discussed the possibility of its being a *Ditylenchus* species. *Tetylenchus* and *Tetylenchinae* Siddiqi, 1970 are therefore regarded as genus et subfamilia dubia.

## Type species

*Tetylenchus tenuis* (Micoletzky, 1922) Filipjev, 1936

syn. *Tylenchus tenuis* Micoletzky, 1922

*Anguillulina tenuis* (Micoletzky) Goodey, 1932

*Tylenchorhynchus tenuis* (Micoletzky) Filipjev, 1936

## Species dubia et incerta sedis

*Tetylenchus dimidius* Kirjanova, 1951

## Note

Several species were assigned to this genus. *Tetylenchus abulbosus* Thorne, 1949 is now the type species of *Atetylenchus*; *T. granulosus* (Cobb, 1893) is senior synonym of *Radopholus similis*; *T. joctus* Thorne, 1949 and *T. productus* Thorne, 1949 are now in *Merlinius*; *T. curiosus* Wilski, 1965 is combined with *Nagelus* and *T. nicotiana* Yokoo & Tanaka in Tanaka & Tsumagori, 1954 is transferred to *Rotylenchulus*.

ETYMOLOGY. From first two letters of the type species name *tenuis*, and *Tylenchus*.

The type species was found in alpine moss, Zirbitzkogel, Steiermark, Austria.

## FAMILY PSILENCHIDAE

The family Psilenchidae has members looking like those in Tylenchidae, particularly in the weak stylet and elongate tail, but the didelphy and the presence of phasmids on the tail clearly differentiate between the two families. Luc *et al.* (1987) and Ryss (1993) regarded *Psilenchus*, *Atetylenchus* and *Antarctenchus* as representing the most primitive taxa of Tylenchida. Sturhan & Rahi (1996) stated that the placement of these genera into a separate, though obviously paraphyletic taxon, Psilenchidae in Dolichodoroidea, as done by Siddiqi (1986) and Ryss (1993), instead of keeping them in closer systematic relationship to Tylenchidae and Anguinidae, appeared more justified.

## Family Psilenchidae Paramonov, 1967 (Khan, 1969)

## Diagnosis

Dolichodoroidea. Small to moderately sized (0.5–1.8 mm). Cuticle distinctly annulated. Lateral field with four incisures, inner ones rarely obscure. Amphidial apertures indistinct, pore-like, near oral opening, or distinct slit-like at base of lip areas. Deirids present. **Phasmids distinct, pore-like, on tail.** Cephalic region generally continuous, finely striated; six inner labial and four cephalic papillae on surface. **Stylet slender, conus much shorter than the shaft**, basal knobs present or absent. Median oesophageal bulb muscular, valvate. Basal bulb offset from intestine; cardia prominent. Vulva median or submedian, with or without lateral membranes. Spermathecae axial (Psilenchinae) or lobed (Antarctenchinae). Ovaries paired, outstretched. **Tails filiform or elongate-conoid, similar between sexes.** **Bursa simple, adanal.** Spicules tylenchoid, cephalated, pointed distally. Gubernaculum simple,

trough-like, fixed. Weak plant parasites; associates of lower plants (excluding fungi) and feeders on root hairs and epidermal cells.

Type subfamily

*Psilenchinae* Paramonov, 1967

Other subfamily

*Antarctenchinae* Spaull, 1972

**Key to subfamilies of *Psilenchinae***

1. Stylet knobbed; vulva with lateral membranes and epiptygma ..... ***Antarctenchinae***
- Stylet not knobbed; vulva without lateral membranes and epiptygma ..... ***Psilenchinae***

**Subfamily *Psilenchinae* Paramonov, 1967**  
**syn. *Leipotylenchinae* Sher, 1974**

Diagnosis

*Psilenchidae*. Cephalic region smooth or annulated, conoid-rounded or broadly rounded; framework lightly sclerotized. Amphid apertures generally distinct, oval slit-like near outer margins of lateral lip areas (indistinct in *Atetylenchus*). Stylet slender, **base not knobbed**; protractors divergent. Orifice of dorsal gland at some distance from stylet base. Vulva near middle of body, **lacking epiptygma or lateral membranes**. Spermathecae axial, elongate. Tails elongate-conoid, filiform or clavate. Bursa large, adanal. Phasmids may extend into bursa. **Hypoptygma absent**. Associates of plant roots and mosses.

Type genus

*Psilenchus* de Man, 1921

Other genus

*Atetylenchus* Khan, 1973

**Key to genera of *Psilenchinae***

1. Cephalic region distinctly annulated; amphidial apertures indistinct, labial; median bulb anterior to middle of oesophagus ..... ***Atetylenchus***
- Cephalic region appearing smooth; amphidial apertures distinct, postlabial; median bulb posterior to middle of oesophagus ..... ***Psilenchus***

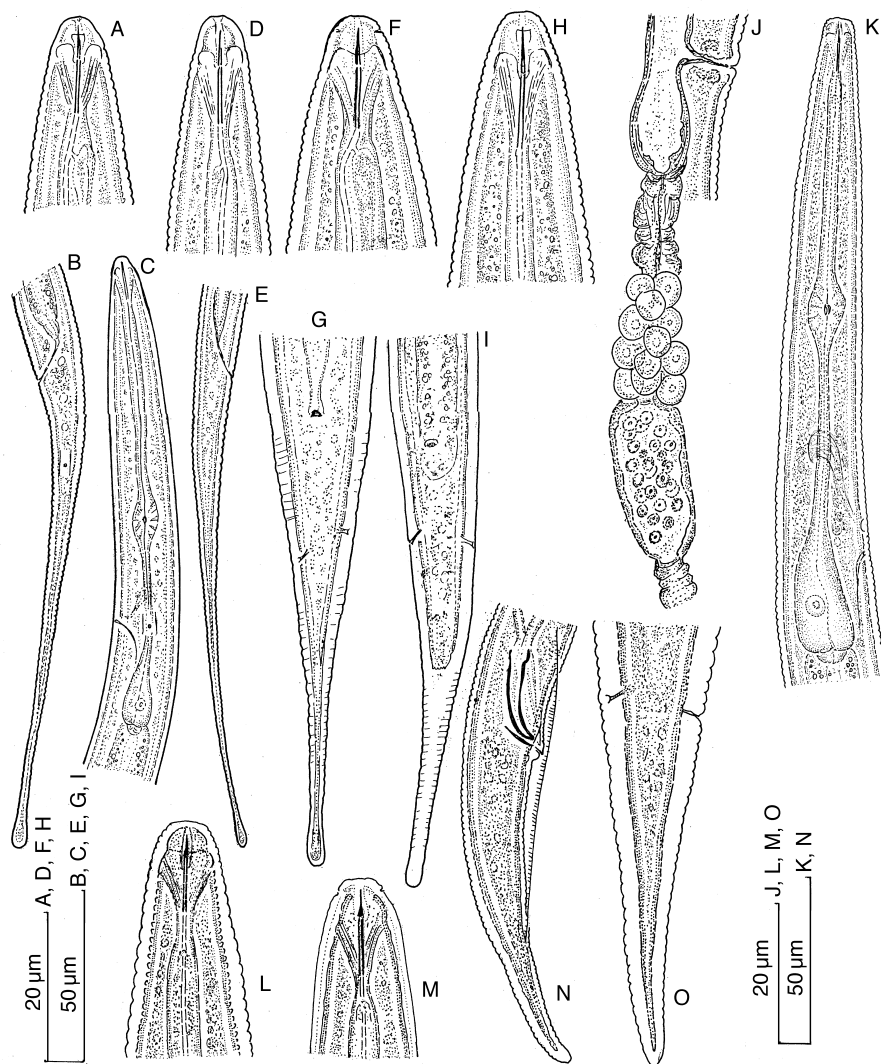
**Genus *Psilenchus* de Man, 1921**

(Fig. 111, A–I)

**Diagnosis**

*Psilenchinae*. Body 0.7–1.7 mm long, usually curved upon relaxation. Lateral fields each with four incisures, inner two may be indistinct or absent. Amphidial apertures transverse, slit-like, at base of lateral lip areas. **Phasmids distinct, on tail, anterior to its middle**. Cephalic region elevated, rounded or conoid, smooth or striated; framework slightly sclerotized, with conspicuous outer margins extending into body. Stylet cylindrical, 10–24  $\mu\text{m}$  long, conus distinctly shorter than shaft, **basal knobs absent**. Median bulb prominent, generally oval, usually behind middle of oesophagus. Basal bulb small, pyriform; cardia discoidal or rounded. Vulva near middle ( $V = 45\text{--}53$ ), lacking epiptygma and lateral membranes. **Ovaries paired**, outstretched in opposite directions. **Spermathecae elongate**, axial. Tail elongate, with clavate or non-clavate rounded tip. Bursa prominent, adanal. Sperm round, moderately large. Spicules tylenchoid, 25–33  $\mu\text{m}$  long. Gubernaculum simple, trough-shaped, fixed.

**Type species***Psilenchus hilarulus* de Man, 1921**Other species***Psilenchus aestuarius* Andr ssy, 1962*P. bahiablancae* Doucet, 1996*P. bilineatus* Mizukubo & Nakasono, 1987*P. clavicaudatus* (Micoletzky, 1922) Thorne, 1949syn. *Tylenchus clavicaudatus* Micoletzky, 1922*Anguillulina clavicaudata* (Micoletzky) Goodey, 1932*Tylenchorhynchus clavicaudatus* (Micoletzky) Filipjev, 1936*Tetylenchus clavicaudatus* (Micoletzky) Filipjev, 1936*P. curcumerus* Rahaman, Ahmad & Jairajpuri, 1994*P. elegans* Thorne & Malek, 1968*P. gigas* Thorne & Malek, 1968*P. hilarus* Siddiqi, 1963syn. *Psilenchus neoformis* Jairajpuri & A.H. Siddiqi, 1963*P. intermedius* Thorne & Malek, 1968*P. iranicus* Kheiri, 1970*P. klingleri* Brzeski, 1989*P. magnificus* Lal & Khan, 1990*P. minor* Siddiqi, 1963*P. mixus* Bajaj, 1998*P. pini* Lal & Khan, 1990*P. pratensis* Doucet, 1996*P. striatus* Thorne, 1949*P. terextremus* Hagemeyer & Allen, 1952*P. vinciguerrae* Brzeski, 1991



**Fig. 111.** A–C. *Psilenchus hilarulus* de Man, female from Hungary. D and E. *Psilenchus minor* Siddiqi, holotype female. F and G. *Psilenchus clavicaudatus* Micoletzky, holotype female (original type slide of Micoletzky from Humboldt University Museum, Berlin). H and I. *Psilenchus aestuarius* Andrassy, female on slide No. 7272 of Andrassy (1962). J–O. *Atetylenchus abulbosus* (Thorne) from California, USA. A, D, F, H, L and M. Head ends of females. B, E, G, I and O. Tail ends of females. C and K. Oesophageal regions of females. J. Posterior reproductive branch of female. N. Tail end of male.



## Notes

*Psilenchus machadoi* Andr ssy, 1963 in Brzeski, 1969 in lapsus calami for *Malenchus machadoi*. Doucet (1996) reported *P. hilarus* from Argentina and two new species and gave a key to the species of *Psilenchus*. A tabular key to *Psilenchus* spp. is given by Brzeski (1989), who described *P. klingleri* from moss soil in Switzerland.

ETYMOLOGY. From the Greek *psilos* = strip, depilate, and *enchos* = spear (for knob-less spear).

The type species was found by de Man in 1920 in moist plant soil at the bank of Mark River near Breda, The Netherlands.

**Genus *Atetylenchus* Khan, 1973**

**syn. *Leipotelenchus* Sher, 1974**

**(= junior objective synonym)**

(Fig. 111, J–O)

## Diagnosis

*Psilenchinae*. Medium-sized (1–1.5 mm). Lateral field with four incisures, not areolated. **Amphidial apertures conspicuous, near oral aperture.** Deirids present. Phasmids pore-like, on tail, not extending into bursa. Cephalic region continuous, rounded, annulated; framework lightly sclerotized. Stylet lacking basal knobs. **Median bulb muscular, anterior to middle of oesophagus.** Basal bulb saccate. Cardia large, rounded. Vulva median. Didelphic, amphidelphic. Spermathecae elongate-oval, axial. Oocytes mostly in a row. Tails in both sexes elongate, tapering, ventrally arcuate, with minutely rounded tip; hyaline terminal portion inconspicuous. Bursa adanal. Spicules cephalated, arcuate. Gubernaculum trough-shaped, fixed.

## Type species

*Atetylenchus abulbosus* (Thorne, 1949) Khan, 1973

syn. *Tetylenchus abulbosus* Thorne, 1949

*Leipotelenchus abulbosus* (Thorne) Sher, 1974

*Psilenchus abulbosus* (Thorne) Bajaj, 1998

## Other species

*Atetylenchus graminus* (Bajaj, Kaushik & Bhatti, 1982) comb. n.

syn. *Psilenchus graminus* Bajaj, Kaushik & Bhatti, 1982

## Species inquirenda

*Leipotelenchus amiri* Maqbool & Shahina, 1985

syn. *Merlinius amiri* (Maqbool & Shahina, 1985) Siddiqi, 1986

*Atetylenchus amiri* (Maqbool & Shahina) Geraert & Raski, 1987

*Antarctenchus amiri* (Maqbool & Shahina) Fatima, Farooq & Khan, 1990

*Psilenchus amiri* (Maqbool & Shahina) Bajaj, 1998

## Note

S.H. Khan (1973a) and Sher (1974) proposed *Atetylenchus* and *Leipotylenchus* for the same species and hence these genera are objective synonyms. Bajaj (1998) synonymized *Atetylenchus* with *Psilenchus*.

ETYMOLOGY. From the Greek privative prefix *a* = without (for stylet knobs), and *Tetylenchus* to which the type species was originally assigned.

The type habitat and locality for the type species is soil in a wheat field near Downey, Idaho, USA.

## Subfamily Antarctenchinae Spaul, 1972

### Diagnosis

Psilenchidae. Cephalic region finely annulated; **framework moderately sclerotized. Amphidial apertures pore-like, labial near oral aperture. Stylet knobbed**, 18–22  $\mu\text{m}$  long in type genus; **protractors tubular**. Orifice of dorsal oesophageal gland close to stylet base. Vulva subequatorial, **with lateral membranes and epiptygma**. Spermathecae round to oval, lobed. **Hypoptygma present**. Tail similar between sexes, elongate, filiform. Bursa adanal. Phasmids pore-like, caudal, not extending into bursa. Associates of mosses.

### Type genus

*Antarctenchus* Spaul, 1972

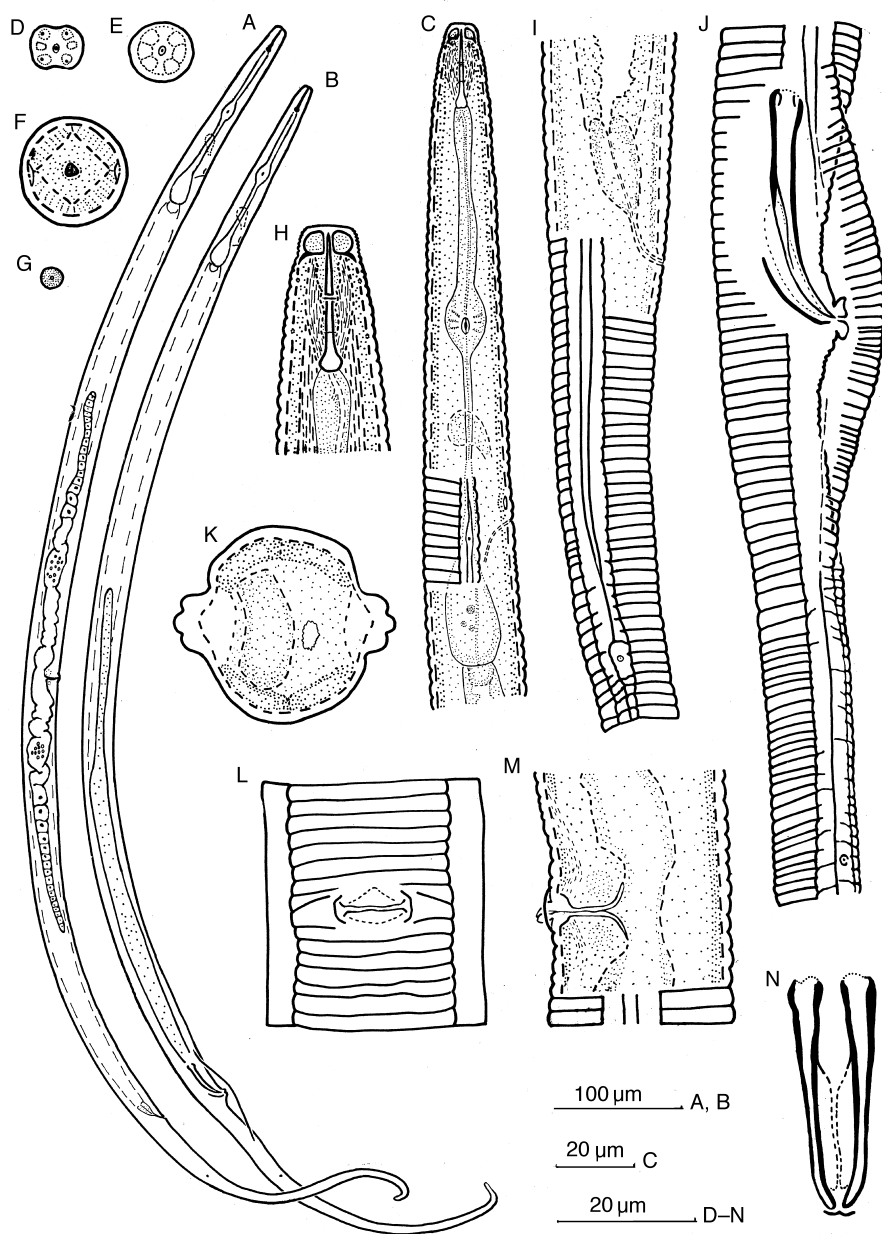
No other genus.

## Genus *Antarctenchus* Spaul, 1972

(Fig. 112)

### Diagnosis

Antarctenchinae. With characters of the subfamily. Body elongate, slender ( $L = 1\text{--}1.3\text{ mm}$ ;  $a = 35\text{--}51$  in type species). Cuticle distinctly annulated; lateral fields each with four incisures, not areolated except towards extremities. Cephalic region slightly flattened dorso-ventrally. Four submedian cephalic papillae and six labial papillae around oval oral opening present on surface. Amphids labial; deirids near excretory pore, behind nerve ring; phasmids anterior to middle of tail, outside the bursa region. **Stylet with compact, slightly flange-like basal knobs**. Median bulb oval, slightly anterior to middle of oesophagus. Vulva at 44–49% of body length in type species, with epiptygma and small lateral membranes. Ovaries outstretched in opposite directions, with oocytes in a row. Tails elongate-filiform, tip conoid to acute. Testis outstretched. Sperm rounded, about 3  $\mu\text{m}$  in diameter. Spicules arcuate, cephalated, 36–41  $\mu\text{m}$  long in type species. Gubernaculum trough-shaped in lateral view, w-shaped in transverse section, 13–15  $\mu\text{m}$  long in type species. Bursa simple, adanal. Cloacal lips raised, with **paired hypoptygmata on anterior and posterior lips**. Eggs 69–96  $\mu\text{m} \times 23\text{--}33\text{ }\mu\text{m}$ . Juveniles generally similar in appearance to adults. Associate of mosses, rarely of grasses, in usually subzero temperatures.



**Fig. 112.** *Antarctenus hooperi* Spaul. A. Female. B. Male. C. Oesophagus of female. D. En face view. E. Cross-section through basal plate. F and G. Cross-section through anterior and posterior parts, respectively of basal swelling of stylet. H. Head end of female. I and J. Anal regions showing lateral field and phasmid. K. Cross-section of body. L and M. Vulval region

in ventral and lateral view, respectively. N. Spicules in ventral view. (After Spaul (1972), courtesy *Nematologica*.)

**Type species**

*Antarctenchus hooperi* Spaul, 1972

No other species.

ETYMOLOGY. From Antarctica, and suffix of *Tylenchus*.

The type species was found on the moss *Andreaea gainii* Card. on Signy Island, South Orkney Islands, Antarctica.

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# VIII Suborder Criconematina

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## SUBORDER CRICONEMATINA SIDDIQI, 1980

### Diagnosis

Tylenchida. Exclusively root-parasitic; **males and some juveniles lack a stylet or have a degenerate one and cannot feed on roots. Marked sexual dimorphism in anterior region manifest.** Cuticle either thin and finely annulated or thick and coarsely annulated; in latter case may have retrorse annules, scales, spines, or an extra cuticular body sheath. Lateral fields present or absent. **Deirids absent** except in juveniles of some Tylenchuloidea. **Phasmids absent.** **Female:** Vermiform, sausage-shaped, or obese only in Tylenchuloidea as root ecto-, rarely endoparasites. Usually under 1 mm (smallest 0.1 mm) long. Cephalic region smooth or usually with one to three coarse annules; **framework hexaradiate**, with light to heavy sclerotization. Oral aperture dorsoventrally oval or slit-like, often appearing **I-shaped due to the presence of two lateral liplets**. Six lip areas, may be fused to form a labial disc (Loof & De Grisse, 1974). **Submedian lip areas with lobe-like outgrowths** in several genera. No sensilla on labial surface; inner labial sensilla open in prestoma. Stylet long or short, **but shaft always about 8–10  $\mu\text{m}$  long**. Basal knobs well developed; **large knobs may characteristically be anchor-shaped**. Orifice of dorsal gland at about 3  $\mu\text{m}$  or more from base of stylet. **Oesophagus criconematoid:** corpus enormously developed, broad-cylindroid with muscular postcorpus amalgamated with precorpus; isthmus either slender and offset from basal bulb (Tylenchuloidea), or broad and amalgamated with it (Criconematoidea, Hemicycliophoroidea); **basal bulb** small, containing three oesophageal glands (except *Tumiota* in which glands are partially free). Oesophago-intestinal valve (cardia) small, usually indistinct. Nerve ring circum-oesophageal. Excretory pore oesophageal or post-oesophageal; **excretory system may produce gelatinous matrix** in which eggs are deposited (e.g. *Tylenchulus*). Intestine syncytial, lacking a definite lumen, often appears as a solid mass, which may extend into tail cavity; junction with rectum indistinct. Rectum obscure, short; anus a small round pore,

rarely absent. Monodelphic, prodelphic. Vulva transversely oval or slit-like, located posteriorly, generally at more than 85% of body from anterior end. Vagina anteriorly directed. **Postvulval uterine sac absent. Spermatheca small, offset, ventral or ventro-lateral to the axis of the gonoduct.** Uterus with a muscular part and a glandular crustaformeria, may be very thick-walled, and in *Meloidoderita* hypertrophied to form a **cystoid body**. **Male:** Vermiform. **Oesophagus degenerate.** Stylet also degenerate, or lacking. Monorchic; gonoduct usually filled by minute round or amoeboid **sperm, which are often produced at one stage near the final moult; testis usually obliterated in adult.** **Bursa weakly developed** (except Hemicycliophoroidea), rarely enveloping tail tip (*Tylenchocriconema*), **absent in several groups** (Tylenchulidae, Sphaeronematidae, most Paratylenchidae). **Spicules setaceous**, often very long, straight, arcuate, U- or hook-shaped. Gubernaculum simple, linear or crescent-like in lateral view, fixed. Cloacal lips narrow, sometimes drawn out as a penial tube (tubus). **Hypoptygma** (cloacal papilla) **single**, rarely double (*Tylenchocriconema*), or absent (*Tylenchulus*). Terrestrial, not marine. Females and most juveniles obligate root ectoparasites, rarely females in some Tylenchuloidea may secondarily become endoparasitic.

#### Type genus

*Criconema* Hofmänner & Menzel, 1914

#### Type superfamily

Criconematoidea Taylor, 1936 (1914)

#### Other superfamilies

Hemicycliophoroidea Skarbilovich, 1959

Tylenchuloidea Skarbilovich, 1947

#### Key to superfamilies of Criconematina

1. Females and juveniles with thick cuticle, bearing coarse, round or retrorse annules; oesophagus with isthmus broad and amalgamated with basal bulb ..... **2**  
 Females and juveniles with thin cuticle bearing fine round annules; oesophagus with isthmus not amalgamated with basal bulb ..... **Tylenchuloidea**
2. Females and juveniles elongate-vermiform, usually over 0.6 mm long; annules round, lacking cuticular outgrowths; male with elongate tail and high bursa, does not develop by metamorphosis ..... **Hemicycliophoroidea**  
 Females and juveniles spindle- or sausage-shaped, usually under 0.5 mm long; annules retrorse (except secondarily becoming rounded in females of most *Hemicriconemoides* spp.), may have cuticular outgrowths; male with short tail and low or no bursa, develops by metamorphosis ..... **Criconematoidea**

#### Remarks

The suborder Criconematina was proposed by Siddiqi (1980b) and assigned to the Tylenchida, which already had two suborders, Tylenchina and Aphelenchina. Siddiqi discussed the characteristics, origin and phylogeny of the Criconematina and pointed out its relationships with the Tylenchina, to which it is more related than

the Aphelenchina (in the same year, Siddiqi proposed a new order for the Aphelenchina, the Aphelenchida).

Criconematina differs from Tylenchina and Hexatylinea, as discussed under these suborders in this book. The group stands out by certain morphological characteristics: retrorse annules with cuticular scales, spines and body sheath in several genera, I-shaped oral aperture, production of gelatinous matrix by the renette cell and males with degenerate oesophagus and stylet, and testis in adults obliterated but vas deferens packed with small rounded sperm. Several characteristics are shared with Hexatylinea, as discussed by Siddiqi (1980b).

Siddiqi (1980) stated that Criconematina might have originated from ancestor with a broad corpus and strong stylet, as found in infective females of some Hexatylinea (*Robleus*, *Deladenus*, *Fergusobia*), which acquire these structures through dimorphism. It would appear likely that, through various selection pressures and neoteny, such Hexatylinea might have become root-parasitic at an early stage of their evolution. The neoteny might have become established and thus the nematodes might have lost their ability to revert back to fungal feeding or insect-parasitism. However, there is no instance of fungal feeding or of insect association in the contemporary Criconematina, which have become root-parasitic *en masse*. The origin of Criconematina is obscure. Two evolutionary lines of Criconematina are evident (see Siddiqi, 1980, 1980b), one representing Tylenchuloidea, the other Criconematoidea and Hemicyclophoroidea (see discussion in Chapter III).

## **SUPERFAMILY CRICONEMATOIDEA TAYLOR, 1936 (1914) (GERAERT, 1966)**

**syn. Criconematoidi Paramonov, 1967 (sub-superfamily name  
amended from Criconematini Paramonov, 1967)**

### **Diagnosis**

Criconematina. Small-sized (seldom over 0.8 mm), showing marked sexual dimorphism. **Females and juveniles sausage- to spindle-shaped with thick cuticle and coarse retrorse annules** (annules secondarily rounded in females of Hemicriconemoidinae and some Criconematinae), **with or without scales, spines and other configurations; males vermiform with not so thick cuticle and annules always rounded** and a degenerate oesophagus hardly showing any structure. **Lateral fields** with incisures in males, **absent in juveniles and females**. Cephalic region of juveniles and females with one or two annules, an indistinct labial disc bearing I-shaped oral aperture surrounded by six pseudolip areas, with or without submedian lobes; no sensory papillae or pits on surface; in males cephalic region usually continuous, rounded and striated, and framework not appearing in lateral view as 'spectacle mark'. Stylet well developed in juveniles (exceptionally absent in some stages) and females. **Conus markedly longer than shaft, latter usually about 10–12  $\mu\text{m}$  long, basal knobs prominent, appearing anchor-shaped**. Orifice of dorsal oesophageal gland 3–6  $\mu\text{m}$  behind stylet base; **stylet absent in males**. Juveniles and females with well-developed criconematoid oesophagi, precorpus broad, posteriorly expanded and continued into a slightly broader, very muscular, postcorpus having large, elongated refractive thickenings; the two parts forming a broad cylindrical

muscular corpus filling the body width. **Isthmus short, broad and amalgamated with a small reduced basal bulb offset from intestine** and containing the three oesophageal glands. A small non-cellular cardia may be present. Excretory pore at, or behind, base of oesophagus. Intestine syncytial, lacking lumen. Vulva far posterior, ovary anteriorly outstretched. Postvulval uterine sac absent. **Male develops by metamorphosis within a sausage-shaped juvenile**. Testis degenerate in adult; gonoduct packed with numerous, very small, round sperms produced at one stage of development. Spicules elongate-setose, almost straight to arcuate, proximally cephalated and distally pointed; gubernaculum simple, fixed. **Male tail short; bursa low**, adanal, subterminal or terminal, occasionally absent. **Juveniles lack a body sheath**. Ectoparasites of roots, males and some juveniles incapable of tissue feeding.

#### Type family

Criconematidae Taylor, 1936 (1914)

No other family.

### FAMILY CRICONEMATIDAE (The ring nematodes)

The ring nematodes have a short, sausage-shaped body that may curve in a ring when relaxed; with about 33–200 thick, retrorse annules and a long stylet which bears anchor-shaped basal knobs. They move sluggishly, crawling like a worm by lengthening and shortening of the body annules, in contrast to the typical undulating motions of other tylenchs (Stauffer, 1924). A large number of species have cuticular outgrowths, such as scales and spines, and *Hemicriconemoides* females have round annules and a cuticular body sheath, but its juveniles have retrorse annules and are scaled.

The ring nematodes are one of the important ectoparasitic nematodes which become a nuisance on certain crops when large populations are built up. They are usually common in sandy soil and in soils with a high pH and feed on the root cortex with the anterior part of the body usually thrust into the tissue.

Species with scales and spines (Criconematinae) are seldom encountered in agricultural land. They mostly parasitize woody perennials in forest and alpine communities. One species, *Ogma rhombosquamatum*, is found in the rhizospheres of *Olea europaea* L., *Pinus* sp. and *Smilax* sp. in Italy. It forms colonies on olive roots and feeds in the cortical tissues two to three cells deep. Feeding causes thickening of the cell walls and hypertrophy of the nucleus and nucleolus and results in necrosis of epidermal and cortical tissue (Vovlas & Inserra, 1981). *Ogma serratum* was described as parasitizing peach trees in the Himalayan foothills in north India (Khan & Siddiqi, 1963).

Members of the Macroposthoniinae and Hemicriconemoidinae do occur on agricultural crops, and also in grassland and on woody perennials. *Macroposthonia ornata* feeding resulted in severely discoloured and necrotic lesions on peanut roots, pods and pegs; in USA, as much as 50% loss in pod yield due to this nematode has been recorded (Minton & Bell, 1969). It is pathogenic to carnation, lucerne and grasses. In India it occurs on several field crops (cabbage, okra, sorghum), and, on



ragi (*Eleusine coracana*), its feeding significantly reduces top and root weights (Acharya & Das, 1983).

*Macroposthonia xenoplax*, which is known to be an important parasite of walnut and peach trees, has recently been found to be an ecto-endoparasite of roots of walnut (Ciancio & Grasso, 1998). Its life cycle is completed in 25–35 days, with four normal moults, of which one occurs inside the egg (Seshadri, 1965). *Macroposthonia xenoplax* is injurious to carnations, concord grapes, peaches and walnuts in California, USA. It is pathogenic to Japanese holly (*Ilex crenata* Thumb.), producing interveinal chlorosis, leaf drop and stunted plants (Aycock *et al.*, 1976). Ring nematodes (mostly *M. onoensis*) are a problem in rice production in Louisiana and Texas and yields in infested areas are low when compared to non-infested areas of Arkansas and California (Hollis & Keoboornueng, 1984). On peach, *M. xenoplax* and *M. ornata* produced the enzyme  $\beta$ -glucosidase and metabolized prunacin, but only *M. xenoplax* increased in number, because it was able to produce  $\beta$ -cyanoalanine synthase to detoxify the cyanide released from prunacin (Nyczepir *et al.*, 1988).

*Macroposthonia ornata* and *Phytophthora megasperma sojae* together caused 48.7% lower soybean yields than *Phytophthora m. sojae* alone. This shows that *M. ornata* predisposes soybean to the attack by this fungus (Campos & Schmitt, 1981).

The taxonomy of this group has undergone upheavals. The *Macroposthonia* spp. discussed above have been shunted from *Criconemoides* to *Macroposthonia*, from the latter to *Criconemella* and from *Criconemella* back to *Macroposthonia*, 'according to whims of taxonomy', as Maggenti (1981, p. 174) rightly put it. The same situation exists with the taxonomy of some other members of the Criconematinae. Hoffmann (1973) rejected Mehta & Raski's (1971) revision of the genus *Criconema* when he described *Criconema proclivis*. I can only hope that my generic and subgeneric listing of these nematodes will improve the situation.

The family Criconematidae was elevated to superfamily by Geraert (1966) to contain, beside this family, Hemicycliophoridae, Paratylenchidae, Sphaeronematidae and Tylenchulidae, and to represent a phylogenetic group. I consider it a natural group sufficiently different from other such groups, viz. Hemicycliophoroidea and Tylenchuloidea.

Khan *et al.* (1976) proposed the family Madinematidae, in which they included these genera: *Criconemella*, *Criconemoides*, *Discocriconemella*, *Macroposthonia*, *Madinema*, *Nothocriconema*, *Nothocriconemoides* and *Xenocriconemella*. They restricted Criconematidae to genera in which females bear cuticular outgrowths, elevated the subgeneric ranks of *Crossonema* (although unnecessarily), *Seriespinula* and *Variasquamata*, and proposed a new genus *Croserinema*. The proposal for Madinematidae was not called for since Macroposthoniidae already existed for its members.

Ogmidae Southern, 1914 is a senior family name to Criconematidae, but the latter is conserved by the provision of ICZN Article 40(b), since Criconematidae replaced Ogmidae before 1961 and had won general acceptance.

Oostenbrink (1960), Siddiqi & Goodey (1964), Loof & De Grisse (1974, 1989), Andr  ssy (1979), Luc & Raski (1981), Raski & Luc (1987) and Ebsary (1991) reviewed the taxonomy of Criconematidae. Loof & De Grisse (1974) traced evolutionary trends in some members and Andr  ssy (1979) discussed phylogenetic relationships of Criconematinae, Hemicriconemoidinae, Hemicycliophorinae and

Macroposthoniinae which he believed represented natural groups and constituted the family Criconematidae.

Species in the genera *Criconema*, *Ogma*, *Criconemoides* and *Paratylenchus* have been grouped into subgenera to understand their inter-relatedness which is the key to their identification. The use of subgenera within brackets does not affect the binomen.

## **Family Criconematidae Taylor, 1936 (1914) (Thorne, 1949)**

**syn. Ogmidae Southern, 1914**

**Macroposthoniidae Skarbilovich, 1959**

**Madinematidae Khan, Chawla & Saha, 1976**

### **Diagnosis**

Criconematoidea. With characters of the superfamily, as above.

### **Type subfamily**

Criconematinae Taylor, 1936 (1914)

### **Other subfamilies**

Hemicriconemoidinae Andr ssy, 1979

Macroposthoniinae Skarbilovich, 1959

### **Key to subfamilies of Criconematidae**

1. Female with a cuticular body sheath of round annules;  
juveniles with scales or spines usually arranged irregularly or  
in alternating rows ..... **Hemicriconemoidinae**  
Female without a cuticular body sheath; scales or spines in juveniles, if present,  
almost always arranged in longitudinal rows ..... **2**
2. Female and juveniles with annules ornamented with scales, spines or other  
appendages (except females of *Criconema*) ..... **Criconematinae**  
Female and juveniles with smooth or crenate annules lacking scales, spines or  
other appendages ..... **Macroposthoniinae**

## **Subfamily Criconematinae Taylor, 1936 (1914)**

**syn. Ogminae Southern, 1914 (Filipjev & Schuurmans**

**Stekhoven, 1941)**

### **Diagnosis**

Criconematidae. **Female:** Body arcuate or ring-like, rarely straight upon relaxation, with 24–200 retrorse annules (may be round in *Criconema*), usually ornamented with scales, spines or finger-like appendages arranged in longitudinal rows or as continuous transverse fringe on annules. No cuticular sheath or lateral fields. Submedian lobes in cephalic region present or absent. Stylet and oesophagus typical of the family. Vulva near anus. Tail short, rounded or conical. **Male:** With two, three

or four incisures in lateral fields. Spicules slender, setose, arcuate. Bursa low, subterminal. Hypoptygma single. **Juveniles: Body annules retrorse, with scales or spines arranged in longitudinal rows or as a transverse fringe.**

### Type genus

*Criconema* Hofmänner & Menzel, 1914

#### Subgenera

*Criconema* Hofmänner & Menzel, 1914

*Amphisbaenema* Orton Williams, 1982

*Nothocriconemella* Ebsary, 1981

*Notholetus* Ebsary, 1981

### Other genera

*Bakernema* Wu, 1964

*Blandicephalanema* Mehta & Raski, 1971

*Crossonema* Mehta & Raski, 1971

*Lobocriconema* De Grisse & Loof, 1965

*Neolobocriconema* Mehta & Raski, 1971

*Ogma* Southern, 1914

#### Subgenera

*Ogma* Southern, 1914

*Croserinema* Khan, Chawla & Saha, 1976

*Macrocriconema* Minagawa, 1986

*Orphreyus* subgen. n.

*Pateracephalanema* Mehta & Raski, 1971

*Seriespinula* Mehta & Raski, 1971

### Key to genera of Criconematinae

1. Cephalic region small knob-like ..... *Blandicephalanema*  
    Cephalic region not knob-like ..... 2
2. Female body annules with scales, spines or finger-like projections ..... 3  
    Female body annules (except in tail region) without scales, spines or finger-like  
    projections ..... 5
3. Cuticular appendages membranous ..... *Bakernema*  
    Cuticular appendages not membranous ..... 4
4. Body annules wavy in outline ..... *Ogma*  
    Body annules circular in outline ..... *Crossonema*
5. Cephalic region with submedian lobes ..... 6  
    Cephalic region without submedian lobes ..... *Criconema*
6. Scales, spines, or other outgrowths present in posterior region of body; vulva  
    closed ..... *Neolobocriconema*  
    Scales, spines, or other outgrowths not present in posterior region of body;  
    vulva mostly open ..... *Lobocriconema*

**Genus *Criconema* Hofmänner & Menzel, 1914**

- syn. *Amphisbaenema* Orton Williams, 1982  
*Cerchnotocriconema* Bernard, 1982  
*Nenocriconema* Darekar & Khan, 1982  
*Nothocriconema* De Grisse & Loof, 1965  
*Nothocriconemella* Ebsary, 1981  
*Notholetus* Ebsary, 1981  
*Paracriconema* Ebsary, 1981

**Diagnosis**

Criconematinae. Females 0.2–0.76 mm long. Annules 37–134, round or retrorse, with smooth or crenate margins. Cephalic region with two annules; lip region elevated, with six pseudolips; submedian lobes poorly developed or usually absent. Stylet 45–132 µm long. **Vulva closed, 3–21 annules from terminus.** VL/VB 0.5–3. **Tail conically pointed**, or rounded. Males with three or four incisures in lateral fields and a low bursa, which may be absent. Fourth-stage juveniles with 8–18 rows of scales, each tipped with a pointed spine.

**Type subgenus**

*Criconema* Hofmänner & Menzel, 1914

**Other subgenera**

*Amphisbaenema* Orton Williams, 1982  
*Nothocriconemella* Ebsary, 1981  
*Notholetus* Ebsary, 1981

**Key to subgenera of *Criconema*  
(based on female)**

1. Cephalic region dome-shaped, pseudolips absent ..... *Amphisbaenema*  
 Cephalic region not dome-shaped, pseudolips present ..... 2
2. Scales, spines, or other outgrowths present in posterior region  
 of body ..... *Notholetus*  
 Scales, spines, or other outgrowths not present in posterior region  
 of body ..... 3
3. Lip annules differentiated from body annules ..... *Criconema*  
 Lip annules not differentiated from body annules ..... *Nothocriconemella*

**Remarks**

The genus *Criconema* was proposed by Hofmänner & Menzel (1914) to receive *Criconema guernei* (= *Eubostrichus guernei* Certes, 1889) and *C. morgense* Hofmänner in Hofmänner & Menzel, 1914. Stiles and Hassall (1920) suggested and Taylor (1936) proposed the designation of Certes's *E. guernei* as the type species of *Criconema*. However, Micoletzky (1925) had unambiguously stated *Criconema morgense* as type of *Criconema*, but this species is the type species of *Criconemoides*. In order to preserve the well known names *Criconema* and *Criconemoides*, Loof (*in litt.*) is approaching ICZN to validate the designation of *E. guernei* as type of *Criconema* by Taylor (1936).

The description and illustrations of *E. guernei* suggest that the species is based on juvenile specimens, as was supposed by Hofmänner & Menzel (1914), Mehta & Raski (1971) and Andrassy (1979). Andrassy (1979) discussed the identity of *C. guernei* and concluded that the identity of not only the species, but the genus *Criconema* is uncertain and regarded *Criconema guernei* and *Criconema* as species dubia and genus dubium, respectively.

Raski *et al.* (1984) described a species from locus typicus of *C. guernei* (Certes), i.e. Tierra del Fuego, Chile, of which, they claim, the juveniles fit the original description of *C. guernei* and the females fit perfectly well with what is known on *Criconema giardi*, the species described by Certes (1889) as '*Dorylaimus Giardi*' in the same publication in which the description of *Eubostrichus guernei* appeared in later pages. They called their species *Criconema giardi* (Certes, 1889) Micoletzky, 1925 and proposed that it must be considered a senior synonym of *C. guernei*, due to page priority, and the type species of the genus *Criconema*. The following main objections to this proposal can be raised.

1. Since *E. giardi* has remained unused as a senior synonym in the primary zoological literature for more than 50 years, this name could have been considered a nomen oblitum (forgotten name) before 1 January 1973 under the provision of Article 23(b), but now it should not be used unless the International Commission on Zoological Nomenclature so directs since the above provision has been withdrawn from the ICZN 3rd edition and Article 79(c) (1) and (2) provides for making an application to the Commission for the rejection of such a nomen oblitum.
2. Serious doubts still exist as to the identity of *E. guernei* Certes. Certes (1889) described and sketched cuticular spines 'arranged in six parallel rows along the body', but the juveniles of the species described by Raski *et al.* (1984) have spines in 10–15 longitudinal rows. Consequently, the spacing of rows in figures given for the two species becomes quite different and it cannot be derived that Certes did not see the other rows of spines. Andrassy (1979) points out that no criconematid is known with six rows of spines, the minimum number being eight (except *Ogma minuta* Kirjanova, 1947, which was reported as having four, but the validity of this number is uncertain). However, *Crossonema dracomontanum* Van den Berg, 1983 has females with six longitudinal rows of spines.
3. Whether the specimens on which the species *Eubostrichus guernei* was based by Certes (1889) represent juveniles or females is debatable. If they represent juveniles, then the identity of the species will remain obscure for ever unless topotypes are found fitting exactly the description given by Certes (1889). If they represent females, then the species belongs in the genus *Ogma*.

Nevertheless, there are sufficient reasons to accept that Raski *et al.* (1984) have rediscovered *Criconema giardi* and have re-established the species by publishing a good description and designating a neotype of it, and that *Criconema guernei* is synonymous with it. For any points of disagreement with this view, the International Commission on Zoological Nomenclature should be approached for a ruling. The name *Criconema* is worth conserving as nomen conservandum since it is the basis of family-group and subordinal names.

*Nothocriconema* was proposed by De Grisse & Loof (1965) as a subdivision of *Criconemoides sensu lato* for species with modified cephalic annules lacking

submedian lobes, a closed vulva overhung by its anterior lip and juveniles with longitudinal rows of scales or spines. On the basis of the last character, *Nothocriconema* was assigned by Andr  ssy (1976, 1979) to Criconematinae separate from the Macroposthoniinae, in which juveniles lack scales, spines or other outgrowths of cuticle. Andr  ssy (1976, 1979) synonymized *Lobocriconema* with *Nothocriconema*. Ebsary (1981c) reinstated *Lobocriconema* and proposed two new genera, *Nothocriconemella* and *Paracriconema*, for 'two morphologically distinct groups of species presently included in *Nothocriconema*'. *Nothocriconemella* and *Notholetus* Ebsary, 1981 are proposed here as subgenera of *Criconema* whereas *Paracriconema* Ebsary, 1981 is considered here as a synonym of *Criconema*.

Mehta & Raski (1971) proposed a new subgenus *Variasquamata* under *Criconema* with *C. (Variasquamata) decalineatum* Chitwood, 1957 as the type species, to contain all the species of the genus *Criconema* except *C. guernei* which was left in the subgenus *Criconema* as the sole representative. *Cerchnotocriconema* Bernard, 1982 is not sufficiently different from *Criconema* and has been synonymized with it. The ornamentation of annules of *Cerchnotocriconema psephinum* Bernard, 1982 is similar to that reported for *Criconema giardi* apud Raski, Luc & Valenzuela (1984) and *C. (C.) jaejuense*. Such crust-like ornamentations also occur in species formerly assigned to *Paracriconema*.

**Subgenus *Criconema* Hofm  nner & Menzel, 1914 (Mehta & Raski, 1971)**

**syn. *Nothocriconema* De Grisse & Loof, 1965**

***Paracriconema* Ebsary, 1981**

***Nenocriconema* Darekar & Khan, 1982**

***Cerchnotocriconema* Bernard, 1982**

(Fig. 113, A–E, H–J)

**Diagnosis**

Genus *Criconema*. Annules 32–98, round, flattened or slightly retrorse posteriorly, thick (6–12  $\mu\text{m}$ ). Cephalic annules two, differentiated from body annules, anterior one usually larger than the posterior one. Stylet 51–120  $\mu\text{m}$  long. Vulva closed, 3–15 annules from terminus; lips conical or anterior lip overhanging. VL/VB 0.5–2.1. Tail conically pointed or conoid-rounded. Juveniles with scales, which may be spine-tipped, arranged in 8–14 longitudinal rows.

**Type species**

*Criconema (Criconema) giardi* (Certes, 1889) Micoletzky, 1925

syn. *Criconema giardi* (Certes, 1889) Micoletzky, 1925

*Dorylaimus giardi* Certes, 1889

*Eubostrichus guernei* Certes, 1889

*Criconema guernei* (Certes) Menzel in Hofm  nner & Menzel, 1914

*Hoplolaimus guernei* (Certes) Menzel, 1917

*Iota guernei* (Certes) Micoletzky, 1925

*Ogma guernei* (Certes) Schuurmans Stekhoven & Teunissen, 1938

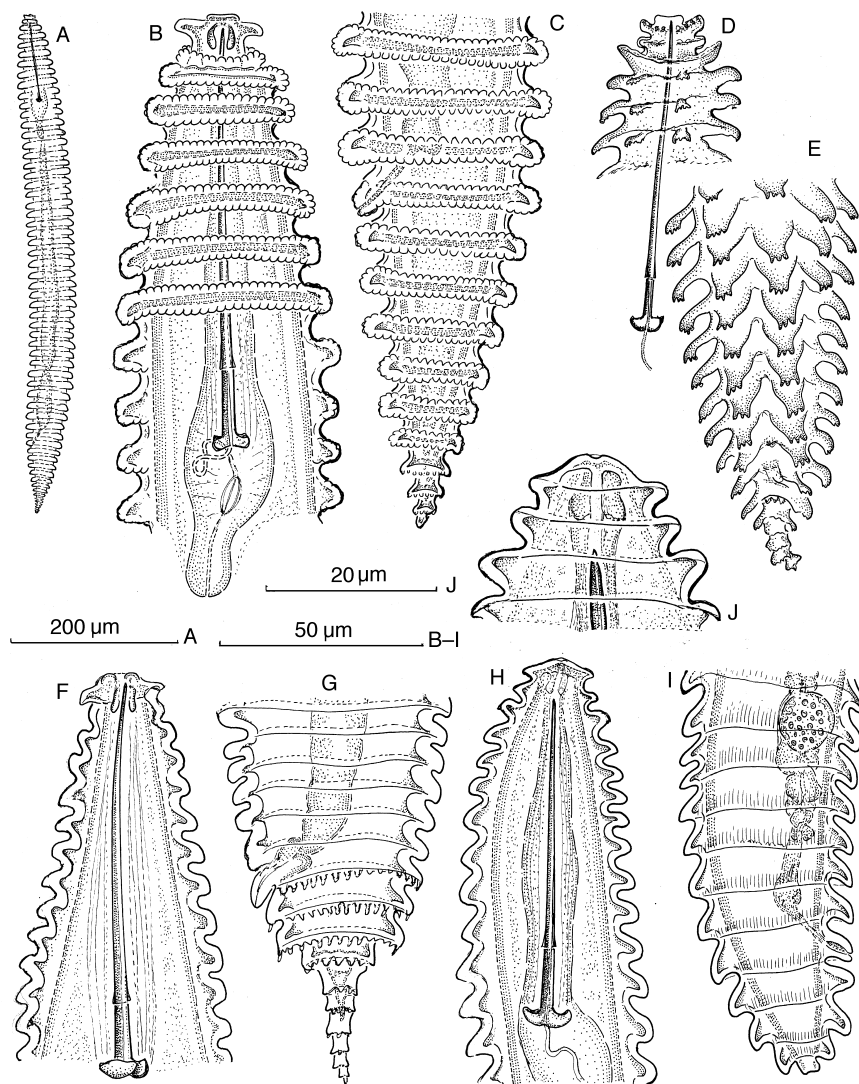


Fig. 113. A–E. *Criconema* (*Criconema*) (= *Cerchnotocriconema*) *psephinum* (Bernard), paratypes. F and G. *Criconema* (*Notholetus*) *spicatus* (Ebsary), paratype. H–J. *Criconema* (*Criconema*) *lamellatum* (Raski & Golden). A. Entire female. B, F, H and J. Head ends of females. C, G and I. Tail ends of females. D and E. Head and tail end of juvenile, respectively.

#### Other species

*Criconema* (*Criconema*) *amicorum* (Orton Williams, 1982) Raski & Luc, 1985  
syn. *Amphisbaenema amicum* Orton Williams, 1982

*Paracriconema amicum* (Orton Williams) Siddiqi, 1986

*C. (C.) annuliferum* (de Man, 1921) Micoletzky, 1925

- syn. *Hoplolaimus annuliferus* de Man, 1921  
*Criconemoides annuliferus* (de Man) Taylor, 1936  
*Nothocriconema* (*Nothocriconema*) *annuliferum* (de Man 1921) De Grisse & Loof, 1965  
*Criconema annuliferum hygrophilum* Andr  ssy, 1952  
*Criconemoides hygrophilus* (Andr  ssy) Oostenbrink, 1960  
*Nothocriconema hygrophilum* (Andr  ssy) De Grisse & Loof, 1965  
*Criconema stygium* Schneider, 1940  
*Criconemoides stygius* (Schneider) Andr  ssy, 1959  
*Nothocriconema stygium* (Schneider) De Grisse & Loof, 1965  
*Criconema kirjanovae* Krall, 1963
- C. (C.) *astakoni* (Ray & Das, 1982) Siddiqi, 1986  
 syn. *Nothocriconema astakoni* Ray & Das, 1982  
*Paracriconema astakoni* (Ray & Das) Siddiqi, 1986
- C. (C.) *aucklandicum* Loof, Wouts & Yeates, 1997
- C. (C.) *bengalense* (Sinha, Baqri & Choudhury, 1991) comb. n.  
 syn. *Nothocriconema bengalense* Sinha, Baqri & Choudhury, 1991
- C. (C.) *boagi* Zell, 1987
- C. (C.) *cardamomi* (Khan & Nanjappa, 1972) Raski & Luc, 1985  
 syn. *Nothocriconema cardamomi* Khan & Nanjappa, 1972
- C. (C.) *certesi* Raski & Valenzuela-A., 1986
- C. (C.) *crisulatum* Loof, Wouts & Yeates, 1997
- C. (C.) *crotaloides* (Cobb, 1924) Schuurmans Stekhoven & Teunissen, 1938  
 syn. *Iota crotaloides* Cobb, 1924  
*Criconema crotaloides* (Cobb) Taylor, 1936  
*Nothocriconema crotaloides* (Cobb) De Grisse & Loof, 1965
- C. (C.) *dorgeski* (Darekar & Khan, 1982) Raski & Luc, 1985  
 syn. *Nenocriconema dorgeski* Darekar & Khan, 1982  
*Paracriconema dorgeski* (Darekar & Khan) Siddiqi, 1986
- C. (C.) *dubium* (De Grisse, 1967) Raski & Luc, 1985  
 syn. *Nothocriconema dubium* De Grisse, 1967  
*Criconemoides dubius* (De Grisse) Luc, 1970  
*Paracriconema dubium* (De Grisse) Ebsary, 1981
- C. (C.) *duplicivestitum* (Andr  ssy, 1963) Raski & Luc, 1985  
 syn. *Criconemoides duplicivestitus* Andr  ssy, 1963  
*Nothocriconema duplicivestitum* (Andr  ssy) De Grisse & Loof, 1965  
*Paracriconema duplicivestitum* (Andr  ssy) Ebsary, 1981
- C. (C.) *indigenae* Van der Berg & Meyer, 1991
- C. (C.) *jaeuense* (Choi & Geraert, 1975) Raski & Luc, 1985  
 syn. *Nothocriconema jaeuense* Choi & Geraert, 1975
- C. (C.) *lamellatum* (Raski & Golden, 1966) Raski & Luc, 1985  
 syn. *Criconemoides lamellatus* Raski & Golden, 1966  
*Nothocriconema lamellatum* (Raski & Golden) De Grisse, 1967  
*Paracriconema lamellatum* (Raski & Golden) Ebsary, 1981  
*Amphisbaenema lamellatum* (Raski & Golden) Orton Williams, 1982
- C. (C.) *lineatum* Loof, Wouts & Yeates, 1997
- C. (C.) *loofi* (De Grisse, 1967) Raski & Luc, 1985



- syn. *Nothocriconema loofi* De Grisse, 1967  
*Criconemoides loofi* (De Grisse) Luc, 1970
- C. (C.) *magnum* Loof, Wouts & Yeates, 1997
- C. (C.) *navarinoense* Raski & Valenzuela-A., 1988
- C. (C.) *neoaxeste* (Jairajpuri & A.H. Siddiqi, 1963) Raski & Luc, 1985  
 syn. *Criconemoides neoaxestis* Jairajpuri & A.H. Siddiqi, 1963  
*Macroposthonia neoaxestis* (Jairajpuri & A.H. Siddiqi) De Grisse & Loof, 1965  
*Lobocriconema neoaxeste* (Jairajpuri & A.H. Siddiqi) De Grisse & Loof, 1967  
*Criconemella neoaxestis* (Jairajpuri & A.H. Siddiqi) Ebsary, 1982  
*Paracriconema neoaxeste* (Jairajpuri & A.H. Siddiqi) Siddiqi, 1986
- C. (C.) *obtusum* (Colbran, 1962) Siddiqi, 1986  
 syn. *Hemicriconemoides obtusus* Colbran, 1962  
*Criconemoides obtusus* (Colbran) Siddiqi & Goodey, 1964  
*Paracriconema obtusum* (Colbran) Siddiqi, 1986
- C. (C.) *orellanai* Raski & Valenzuela-A., 1988
- C. (C.) *osornoense* Raski & Valenzuela-A., 1988
- C. (C.) *palliatum* (Minagawa, 1981) Raski & Luc, 1985  
 syn. *Nothocriconema palliatum* Minagawa, 1981
- C. (C.) *petasum* (Wu, 1965) Raski & Luc, 1985  
 syn. *Criconemoides petasus* Wu, 1965  
*Nothocriconema petasum* (Wu) De Grisse & Loof, 1965
- C. (C.) *princeps* (Andrássy, 1962) Raski & Luc, 1985  
 syn. *Criconemoides princeps* Andrássy, 1962  
*Nothocriconema princeps* (Andrássy) De Grisse & Loof, 1965
- C. (C.) *proteae* Van der Berg & Meyer, 1991
- C. (C.) *psephinum* (Bernard, 1982) Raski & Luc, 1985  
 syn. *Cerchnotocriconema psephinum* Bernard, 1982
- C. (C.) *rarum* (Boonduang & Ratanaprapa, 1974) Raski & Luc, 1985  
 syn. *Lobocriconema rarum* Boonduang & Ratanaprapa, 1974  
*Nothocriconema rarum* (Boonduang & Ratanaprapa) Andrássy, 1974  
*Paracriconema rarum* (Boonduang & Ratanaprapa) Ebsary, 1981
- C. (C.) *robustum* Wang & Wu, 1993
- C. (C.) *sabulosum* (Eroshenko, 1981) Raski & Luc, 1985  
 syn. *Criconemoides sabulosus* Eroshenko, 1981  
*Paracriconema sabulosum* (Eroshenko, 1981) Siddiqi, 1986
- C. (C.) *sanctusfrancisci* (Van den Berg & Heyns, 1977) Raski & Luc, 1985  
 syn. *Nothocriconema sanctifrancisci* Van den Berg & Heyns, 1977
- C. (C.) *shepherdiae* (Jairajpuri & Southey, 1984) Raski & Luc, 1985  
 syn. *Nothocriconema shepherdiae* Jairajpuri & Southey, 1984  
*Paracriconema shepherdiae* (Jairajpuri & Southey) Siddiqi, 1986
- C. (C.) *simplex* Marais & Van den Berg, 1996
- C. (C.) *solitarium* (De Grisse, 1967) Raski & Luc, 1985  
 syn. *Nothocriconema solitarium* De Grisse, 1967  
*Criconemoides solitarius* (De Grisse) Luc, 1970  
*Paracriconema solitarium* (De Grisse) Ebsary, 1981
- C. (C.) *talanum* (Van den Berg, 1984) Siddiqi, 1986  
 syn. *Paracriconema talanum* Van den Berg, 1984

- C. (C.) tribule* (Raski & Golden, 1966) Siddiqi, 1986 (valid sp. for Zell, 1987)  
 syn. *Criconemoides tribulis* Raski & Golden, 1966  
*C. (C.) velatum* (Mehta, Raski & Valenzuela, 1983) Raski & Luc, 1985  
 syn. *Bakernema velatum* Mehta, Raski & Valenzuela, 1983  
*Neobakernema velatum* (Mehta, Raski & Valenzuela) Siddiqi, 1986

#### Species inquirendae et dubiae

- Criconema lepidotum* Skwarra, 1921  
 syn. *Ogma lepidota* (Skwarra) Schuurmans Stekhoven & Teunissen, 1938  
*C. minor* (Schneider, 1940) de Coninck, 1943  
 syn. *Iota minor* Schneider, 1940  
*C. paxi* (Schneider, 1940) de Coninck, 1943  
 syn. *Iota paxi* Schneider, 1940  
*C. southerni* (Schneider, 1940) de Coninck, 1943  
 syn. *Iota southerni* Schneider, 1940  
*C. spinalineatum* Chitwood, 1957

#### Note

The entire cuticle of the females of some *Criconema* spp. may be encrusted with extracuticular deposits of no taxonomic significance. There is a tendency in this group for the outer layers of the cuticle to detach occasionally from most of the body, e.g. *C. obtusum*.

ETYMOLOGY. From the Greek *krikos* = ring (for prominent body annules or, less probably, ring-shaped death position), and *nema* = nematode.

The type species was described from soil in Tierra del Fuego, Chile.

#### Subgenus *Nothocriconemella* Ebsary, 1981

(Fig. 114, A)

#### Diagnosis

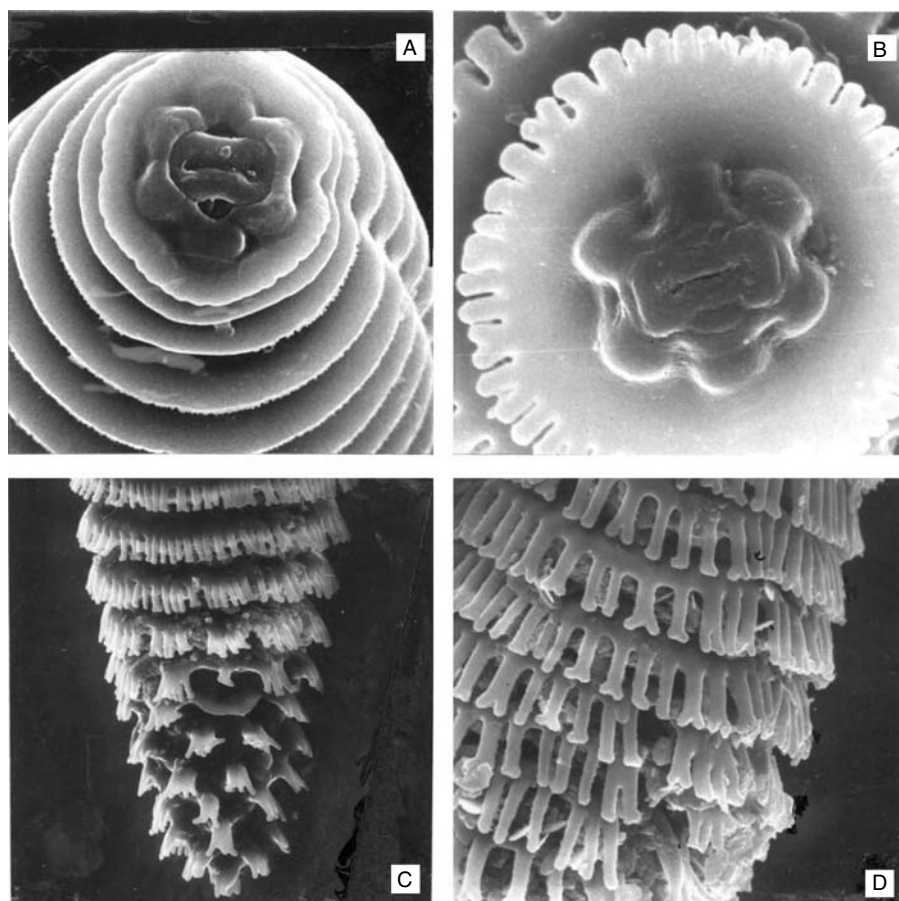
Genus *Criconema*. Annules 59–134, averaging more than 70; 4–6 µm thick, **generally retrorse**. **Cephalic annules not differentiated from body annule, anterior annule narrower than posterior**. Stylet 50–132 µm long, flexible if long. Vulva lips conical, 9–21 annules from tip. VL/VB 0.9–3. Tail conically pointed or conically rounded. Juveniles with smooth scales (minutely spined scales in *C. (N.) orientale*.)

#### Type species

*Nothocriconemella sphagni* (Micoletzky, 1925) Ebsary, 1981

#### Present status

- Criconema (Nothocriconemella) sphagni* Micoletzky, 1925  
 syn. *Criconema sphagni* Micoletzky, 1925  
*Criconemoides sphagni* (Micoletzky) Taylor, 1936  
*Nothocriconema sphagni* (Micoletzky) De Grisse & Loof, 1965  
*Nothocriconemella sphagni* (Micoletzky) Ebsary, 1981



**Fig. 114.** Scanning electron micrographs. A. *Criconema* (*Nothocriconemella*) *sphagni* Micoletzky. B–D. *Crossonema civellae* (Steiner). A and B. Female heads. C. Posterior region showing spines, scales and vulva. D. Female spines on midbody. (A–D. After Ebsary (1981), courtesy *Canadian Journal of Zoology*.)

*Criconemoides grassator* Adams & Lapp, 1967  
*Nothocriconema grassator* (Adams & Lapp) De Grisse, 1967  
*Nothocriconemella grassator* (Adams & Lapp) Ebsary, 1981  
*Criconema grassator* (Adams & Lapp) Siddiqi, 1986

#### Other species

*Criconema* (*Nothocriconemella*) *acriculum* (Raski & Pinochet, 1976) Raski & Luc, 1985  
 syn. *Nothocriconema acriculum* Raski & Pinochet, 1976  
*Nothocriconemella acricula* (Raski & Pinochet) Ebsary, 1981  
*C. (N.) acuticaudatum* Loof, Wouts & Yeates, 1997  
 syn. *Criconema acuticaudatum* Loof, Wouts & Yeates, 1997  
*Nothocriconemella acuticaudata* (Loof, Wouts & Yeates, 1997) comb. n.

- C. (N.) *alpinum* Loof, Wouts & Yeates, 1997  
 syn. *Criconema alpinum* Loof, Wouts & Yeates, 1997  
*Nothocriconemella alpina* (Loof, Wouts & Yeates, 1997) comb. n.
- C. (N.) *ananas* (Heyns, 1970) Siddiqi, 1986  
 syn. *Discocriconemella ananas* Heyns, 1970  
*Nothocriconema ananas* (Heyns) Loof & De Grisse, 1973  
*Nothocriconemella ananas* (Heyns) Van den Berg, 1984
- C. (N.) *bellatulum* (Minagawa, 1981) Raski & Luc, 1985  
 syn. *Nothocriconema bellatulum* Minagawa, 1981  
*Nothocriconemella bellatula* (Minagawa) Siddiqi, 1986
- C. (N.) *calvum* (Raski & Golden, 1966) Raski & Luc, 1985  
 syn. *Criconemoides calvus* Raski & Golden, 1966  
*Nothocriconema calvum* (Raski & Golden) De Grisse, 1967  
*Nothocriconemella calva* (Raski & Golden) Ebsary, 1981  
*Criconema calvum* (Raski & Golden) Raski & Luc, 1985
- C. (N.) *coorgi* (Khan & Nanjappa, 1972) Raski & Luc, 1985  
 syn. *Nothocriconema coorgi* Khan & Nanjappa, 1972  
*Nothocriconemella coorgi* (Khan & Nanjappa) Ebsary, 1981
- C. (N.) *cylindraceum* (Ivanova & Shagalina, 1986) Raski & Luc, 1987  
 syn. *Nothocriconemella cylindracea* Ivanova & Shagalina, 1986
- C. (N.) *degrissei* (Baqri, 1979) Raski & Luc, 1985  
 syn. *Nothocriconema degrissei* Baqri, 1979  
*Nothocriconemella degrissei* (Baqri) Ebsary, 1981
- C. (N.) *demani* Micoletzky, 1925  
 syn. *Criconema demani* Micoletzky, 1925  
*Criconemoides demani* (Micoletzky) Taylor, 1936  
*Nothocriconema demani* (Micoletzky) De Grisse & Loof, 1965  
*Nothocriconemella demani* (Micoletzky) Ebsary, 1981  
*Criconemoides ravidus* Raski & Golden, 1966  
*Criconema ravidum* (Raski & Golden) Siddiqi, 1986
- C. (N.) *graminicola* Loof, Wouts & Yeates, 1997  
 syn. *Criconema graminicola* Loof, Wouts & Yeates, 1997  
*Nothocriconemella graminicola* (Loof, Wouts & Yeates, 1997) comb. n.
- C. (N.) *ina* (Skwiercz, 1983) Raski & Luc, 1985  
 syn. *Nothocriconemella ina* Skwiercz, 1983
- C. (N.) *justum* (Eroshenko, 1982) Siddiqi, 1986  
 syn. *Nothocriconemoides justus* Eroshenko, 1982  
*Criconemella justa* (Eroshenko) Raski & Luc, 1987  
*Mesocriconema justum* (Eroshenko) Ebsary, 1991  
*Nothocriconemella justa* (Eroshenko) Siddiqi, 1986
- C. (N.) *kovacsi* (Andrássy, 1963) Siddiqi, 1986  
 syn. *Criconemoides kovacsi* Andr  ssy, 1963  
*Nothocriconema kovacsi* (Andr  ssy) De Grisse & Loof, 1965  
*Nothocriconemella kovacsi* (Andr  ssy) Ebsary, 1981
- C. (N.) *lanxifrons* (Orton Williams, 1982) Raski & Luc, 1985  
 syn. *Nothocriconema lanxifrons* Orton Williams, 1982
- C. (N.) *longulum* Gunhold, 1953

- syn. *Criconemoides longulus* (Gunhold) Oostenbrink, 1960  
*Nothocriconema longulum* (Gunhold) De Grisse & Loof, 1965  
*Nothocriconemella longula* (Gunhold) Ebsary, 1981  
*Criconema elegantulum* Gunhold, 1953  
*Criconemoides elegantulus* (Gunhold) Oostenbrink, 1960  
*Nothocriconemella elegantula* (Gunhold) Siddiqi, 1986  
*Criconemoides quasidemani* Wu, 1965  
*Nothocriconema quasidemani* (Wu) De Grisse & Loof, 1965  
*Criconema quasidemani* (Wu) Siddiqi, 1986  
*Nothocriconemella quasidemani* (Wu) Siddiqi, 1986
- C. (N.) *macilentum* (Raski & Pinochet, 1976) Raski & Luc, 1985  
syn. *Nothocriconema macilentum* Raski & Pinochet, 1976  
*Nothocriconemella macilenta* (Raski & Pinochet) Ebsary, 1981
- C. (N.) *meridianum* (Mehta, Raski & Valenzuela, 1983) Siddiqi, 1986  
syn. *Criconemella meridiana* Mehta, Raski & Valenzuela, 1983  
*Nothocriconemella meridiana* (Mehta, Raski & Valenzuela) Siddiqi, 1986  
*Mesocriconema meridianum* (Mehta et al.) Loof & de Grisse, 1989
- C. (N.) *miscanthi* (Minagawa, 1982) Raski & Luc, 1985  
syn. *Nothocriconema miscanthi* Minagawa, 1982  
*Nothocriconemella miscanthi* (Minagawa) Siddiqi, 1986
- C. (N.) *montanum* (Razjivin, 1974) Siddiqi, 1986  
syn. *Nothocriconema montanum* Razjivin, 1974  
*Nothocriconemella montana* (Razjivin) Siddiqi, 1986
- C. (N.) *mutabile* (Taylor, 1936) Raski & Luc, 1985  
syn. *Criconemoides mutabilis* Taylor, 1936  
*Nothocriconema mutabile* (Taylor) De Grisse & Loof, 1965  
*Nothocriconemella mutabilis* (Taylor) Ebsary, 1981  
*Criconemoides raskii* Goodey, 1963  
*Criconema raskii* (Goodey) Siddiqi, 1986  
*Nothocriconemella raskii* (Goodey) Siddiqi, 1986  
*Criconemoides siddiqii* Khan, 1964  
*Criconema siddiqii* (Khan) Siddiqi, 1986  
*Nothocriconemella siddiqii* (Khan) Siddiqi, 1986  
*Criconemoides magnoliae* Edward & Misra, 1964  
*Criconema magnoliae* (Edward & Misra) Siddiqi, 1986  
*Criconemoides californicus* Diab & Jenkins, 1966  
*Criconema californicum* (Diab & Jenkins) Siddiqi, 1986  
*Nothocriconemella californica* (Diab & Jenkins) Siddiqi, 1986  
*Criconemoides kashmirensis* Mahajan & Bijral, 1973  
*Criconema kashmirensis* (Mahajan & Bijral) Siddiqi, 1986  
*Nothocriconemella kashmirensis* (Mahajan & Bijral) Siddiqi, 1986
- C. (N.) *neopacificum* (Mehta, Raski & Valenzuela, 1983) Raski & Luc, 1985  
syn. *Nothocriconema neopacificum* Mehta, Raski & Valenzuela, 1983  
*Nothocriconemella neopacifica* (Mehta, Raski & Valenzuela) Siddiqi, 1986
- C. (N.) *orientale* (Andrássy, 1970) Raski & Luc, 1985  
syn. *Nothocriconema orientale* Andrássy, 1970  
*Nothocriconemella orientalis* (Andrássy) Ebsary, 1981

- C. (N.) pacificum* (Andrássy, 1965) Raski & Luc, 1985  
 syn. *Criconemoides pacificus* Andrásy, 1965  
*Nothocriconema pacificum* (Andrássy) Andrásy, 1967  
*Nothocriconemella pacifica* (Andrássy) Ebsary, 1981  
*Criconemoides arcanus* Raski & Golden, 1966  
*Nothocriconema arcanum* (Raski & Golden) De Grisse, 1967  
*Criconema arcanum* (Raski & Golden) Siddiqi, 1986  
*Nothocriconemella arcana* (Raski & Golden) Siddiqi, 1986
- C. (N.) paraguayense* (Andrássy, 1968) Raski & Luc, 1985  
 syn. *Nothocriconema paraguayense* Andrásy, 1968  
*Criconemoides paraguayensis* (Andrássy) Luc, 1970  
*Nothocriconemella paraguayensis* (Andrássy) Ebsary, 1981
- C. (N.) pasticum* (Raski & Pinochet, 1976) Raski & Luc, 1985  
 syn. *Nothocriconema pasticum* Raski & Pinochet, 1976  
*Nothocriconemella pastica* (Raski & Pinochet) Ebsary, 1981
- C. (N.) permistum* (Raski & Golden, 1966) Raski & Luc, 1985  
 syn. *Criconemoides permistus* Raski & Golden, 1966  
*Nothocriconema permistum* (Raski & Golden) De Grisse, 1967  
*Nothocriconemella permista* (Raski & Golden) Ebsary, 1981
- C. (N.) polynesianum* (Orton Williams, 1982) Raski & Luc, 1985  
 syn. *Nothocriconema polynesianum* Orton Williams, 1982  
*Nothocriconemella polynesiiana* (Orton Williams) Siddiqi, 1986
- C. (N.) psammophilum* (Krnjaic & Loof, 1973) Raski & Luc, 1985  
 syn. *Nothocriconema psammophilum* Krnjaic & Loof, 1973  
*Nothocriconemella psammophila* (Krnjaic & Loof) Ebsary, 1981
- C. (N.) sulcitum* (Van den Berg, 1984) Siddiqi, 1986  
 syn. *Nothocriconemella sulcita* Van den Berg, 1984
- C. (N.) undulatum* Loof, Wouts & Yeates, 1997  
 syn. *Criconema undulatum* Loof, Wouts & Yeates, 1997  
*Nothocriconemella undulata* Loof, Wouts & Yeates, 1997
- C. (N.) varicaudatum* (Eroshenko, 1980) Siddiqi, 1986  
 syn. *Nothocriconema varicaudatum* Eroshenko, 1980
- C. (N.) varigatum* Khan, Singh & Lal, 1998  
 syn. *Criconema varigatum* Khan, Singh & Lal, 1998  
*Nothocriconemella varigata* (Khan, Singh & Lal) comb. n.
- C. (N.) yakushimense* Toida, 1983  
 syn. *Nothocriconema yakushimense* Toida, 1983  
*Nothocriconemella yakushimensis* (Toida) comb. n.

## Note

Yeates *et al.* (1997) and Wouts (2000) recognized *Nothocriconemella* as a subgenus of *Criconema*, described four new species of *C. (Nothocriconemella)* and gave a key to its nominal species. The new species described by Wouts (2000) are: *C. (N.) crosbyi* Wouts 2000; *C. (N.) farnelli* Wouts, 2000; *C. (N.) dugdalei* Wouts 2000; and *C. (N.) ramsayi* Wouts, 2000.

ETYMOLOGY. From Greek *nothos* = false, and *Criconemella*.

The type species was collected by Micoletzky (1925) from sphagnum (moss) from Gribsee-Moor and Gadenwant-Moor, Denmark.

### **Subgenus *Amphisbaenema* Orton Williams, 1982**

(Fig. 115, A–H)

#### **Diagnosis**

Genus *Criconema*. Body 0.28–0.44  $\mu\text{m}$  long, with 37–61 coarse annules bearing extracuticular incrustation showing minute dot-like structures cemented on surface. Cephalic region with one dome-shaped annule, sometimes constricted in middle; perioral disc present; pseudolips or submedian lobes absent. Stylet 70–79  $\mu\text{m}$  (75  $\mu\text{m}$ ) long in type species. Vulva closed; anterior lip overhanging vulva. Tail bluntly rounded. Male 0.34–0.38 mm long, with annulated, continuous cephalic region lacking pseudolips and submedian lobes, three incisures in lateral field and a large papilla immediately behind cloacal aperture. Bursa well developed, terminal. Spicules setose, semicircular, 25–29  $\mu\text{m}$  long along the median line. Fourth-stage juveniles with eight rows of large tubercles, each tubercle bearing a spine-like scale visible in optical section.

#### **Type species**

*Criconema* (*Amphisbaenema*) *paradoxiger* (Orton Williams, 1982) Raski & Luc, 1985

syn. *Amphisbaenema paradoxiger* Orton Williams, 1982

*Paracriconema paradoxiger* (Orton Williams) Siddiqi, 1986

*Criconema paradoxiger* (Orton Williams) Raski & Luc, 1985

No other species.

#### **Note**

Decraemer and Geraert (1992) gave the SEM and TEM of the cuticle structure of *Criconema paradoxiger* and Decraemer *et al.* (1996) considered it as the sole species of the genus *Amphisbaenema*, which they recognized on the shape and structure of the lip region.

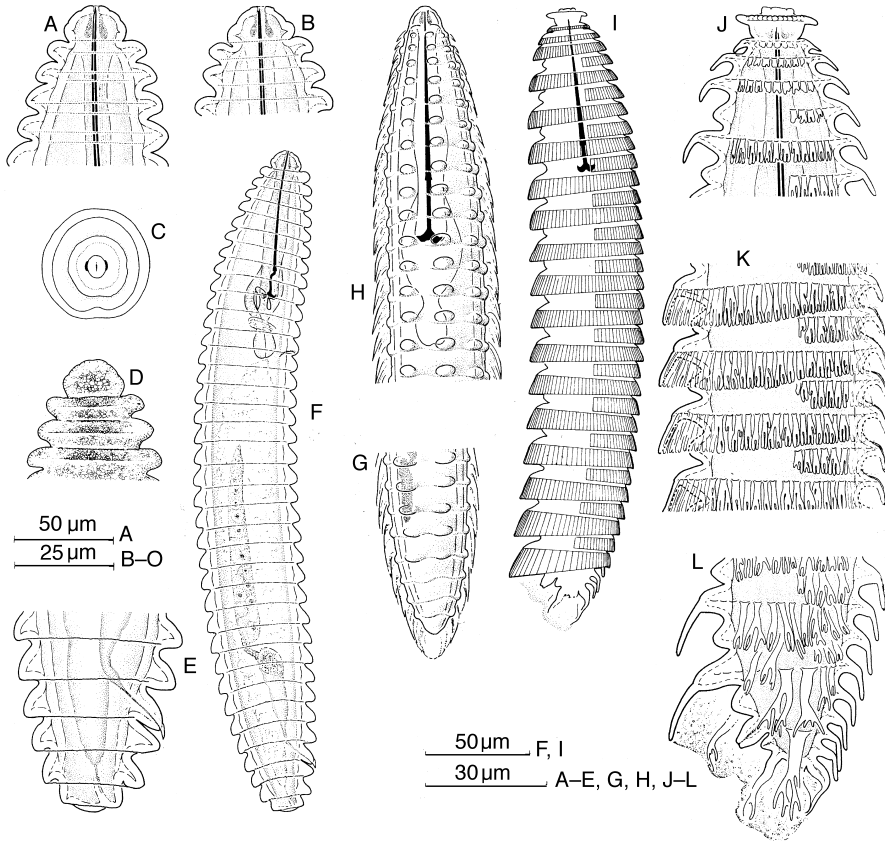
The type species was found in soil around the roots of kava, *Piper methysticum*, at Tapu'ele'ele, Island of Savai'i, Western Samoa.

### **Subgenus *Notholetus* Ebsary, 1981**

(Fig. 113, F & G)

#### **Diagnosis**

Genus *Criconema*. Female 0.31–0.68 mm long. Annules smooth, round or retrorse, 49–86 in number, 5–9  $\mu\text{m}$  wide at midbody, smooth except in posterior region, where scales, spines or cuticular lobes are present. Cephalic region with one or two annules, offset from body, lip region elevated, with pseudolips; submedian lobes absent. Stylet robust, 45–106  $\mu\text{m}$  long. Vulva closed, 6–14 annules from tail terminus. **Tail end conically pointed or spicate, with spines, lobes or other cuticular configurations.** Fourth-stage juveniles with 12–18 rows of scales at midbody, scales being smooth or bearing refractive elements.



**Fig. 115.** A–H. *Criconema* (*Amphisbaenema*) *paradoxiger* (Orton Williams). I–L. *Ogma* (*Orphreyus*) *orphreyifer* (Orton Williams, 1985). A, B, D and J. Head ends of female. C. En face view. E and L. Posterior regions of female. G. Posterior region of juvenile. F and I. Females. H. Cuticular pattern on anterior end of juvenile. K. Cuticular pattern at midbody of female. (After Orton Williams, 1982, 1985.)

#### Type species

*Notholetus spicatus* Ebsary, 1981

#### Present status

*Criconema* (*Notholetus*) *spicatum* (Ebsary, 1981) Luc & Raski, 1985

syn. *Notholetus spicatus* Ebsary, 1981

*Criconema spicatum* (Ebsary) Luc & Raski, 1985

#### Other species

*Criconema* (*Notholetus*) *carolinae* Van den Berg, 1992

syn. *Criconema carolinae* Van den Berg, 1992

*Notholetus carolinae* (Van den Berg) comb. n.

*C. (Notholetus) corbetti* (De Grisse, 1967) Raski & Luc, 1985



- syn. *Nothocriconema corbetti* De Grisse, 1967  
*Criconemoides corbetti* (De Grisse) Luc, 1970  
*Notholetus corbetti* (De Grisse) Ebsary, 1981  
*Criconema corbetti* (De Grisse) Raski & Luc, 1985  
*Lobocriconema patelliferum* Heyns, 1970  
*Criconema patelliferum* (Heyns) Raski & Luc, 1985  
*C. (Notholetus) natalense* (Van den Berg, 1984) Siddiqi, 1986  
syn. *Notholetus natalensis* Van den Berg, 1984  
*C. (Notholetus) sirgeli* Van den Berg & Meyer, 1982  
syn. *Criconema sirgeli* Van den Berg & Meyer, 1982  
*Notholetus sirgeli* (Van den Berg & Meyer) comb. n.  
*C. (Notholetus) spinicaudatum* (Raski & Pinochet, 1976) Raski & Luc, 1985  
syn. *Nothocriconema spinicaudatum* Raski & Pinochet, 1976  
*Notholetus spinicaudatus* (Raski & Pinochet) Ebsary, 1981  
*Criconema spinicaudatum* (Raski & Pinochet) Raski & Luc, 1985  
*C. (Notholetus) victoriae* (Heyns, 1970) Raski & Luc, 1985  
syn. *Nothocriconema victoriae* Heyns, 1970  
*Notholetus victoriae* (Heyns) Ebsary, 1981  
*Criconema victoriae* (Heyns) Raski & Luc, 1985  
*C. (Notholetus) zeae* (Van den Berg & Heyns, 1977) Raski & Luc, 1985  
syn. *Lobocriconema zeae* Van den Berg & Heyns, 1977  
*Notholetus zeae* (Van den Berg & Heyns) Ebsary, 1981  
*Criconema zeae* (Van den Berg & Heyns) Raski & Luc, 1985

ETYMOLOGY. Greek *nothos* = false, *lethe* = oblivion, Latin *letum* = death (author of the genus indicated, *in litt.*, that the name *Notholetus* was coined to show its relationship with *Nothocriconema*).

The type species was found in moss packing about the roots of orchids from Hawaii intercepted in Canada. Ebsary (1981) gave a key to *Notholetus* spp.

### Genus *Ogma* Southern, 1914

syn. *Croserinema* Khan, Chawla & Saha, 1976

*Macrocriconema* Minagawa, 1986

*Orphreyus* gen. n.

*Pateracephalanema* Mehta & Raski, 1971

*Pellipecten* Siddiqi, 1986

*Pseudocriconema* Minagawa, 1984

*Seriespinula* Mehta & Raski, 1976 (Khan, Chawla & Saha, 1976)

*Syro* Orton Williams, 1985

*Variasquamata* Mehta & Raski, 1971 (Khan, Chawla & Saha, 1976)

### Diagnosis

Criconematinae. Female 0.24–0.86 mm long, with 50–94 annules. Annules wavy in outline, with scale-like outgrowths broadly rounded at tip or with one to five spine-like projections, and arranged in 8–21 longitudinal rows on most of body. Cephalic region offset, with one or two annules which may be smooth, crenate or

lobed; anterior annule often larger than posterior; submedian lobes usually present. Stylet 48–125  $\mu\text{m}$ . **Vulva closed, lips conical**, 3–19 annules from terminus. Tail conical or rounded. Males with three or four incisures in lateral field and 28–47  $\mu\text{m}$  long arcuate spicules. Fourth-stage juveniles with scales arranged in longitudinal rows.

#### Type subgenus

*Ogma* Southern, 1914

#### Other subgenera

*Croserinema* Khan, Chawla & Saha, 1976

*Macrocriconema* Minagawa, 1986

*Orphreyus* subgen. n.

*Pateracephalanema* Mehta & Raski, 1971

*Seriespinula* Mehta & Raski, 1971

#### Key to subgenera of *Ogma* (based on females)

1. Size and arrangement of spines different in dorsal and ventral sectors of body ..... *Orphreyus*  
Size and arrangement of spines not different in dorsal and ventral sectors of body ..... 2
2. Lip region with distinct submedian lobes ..... 3  
Lip region without distinct submedian lobes ..... 4
3. Scale-like outgrowths without spine-like appendages, not modified in posterior region ..... *Ogma*  
Scale-like outgrowths with spine-like appendages, modified in posterior region ..... *Macrocriconema*
4. Scale-like outgrowths on annules alternate with those on adjacent annules ..... *Croserinema*  
Scale-like outgrowths on annules not alternating ..... 5
5. Cephalic region with one large and discoidal annule; tail end rounded ..... *Pateracephalanema*  
Cephalic region with two annules; tail end conical, pointed ..... *Seriespinula*

#### Subgenus *Ogma* Southern, 1914

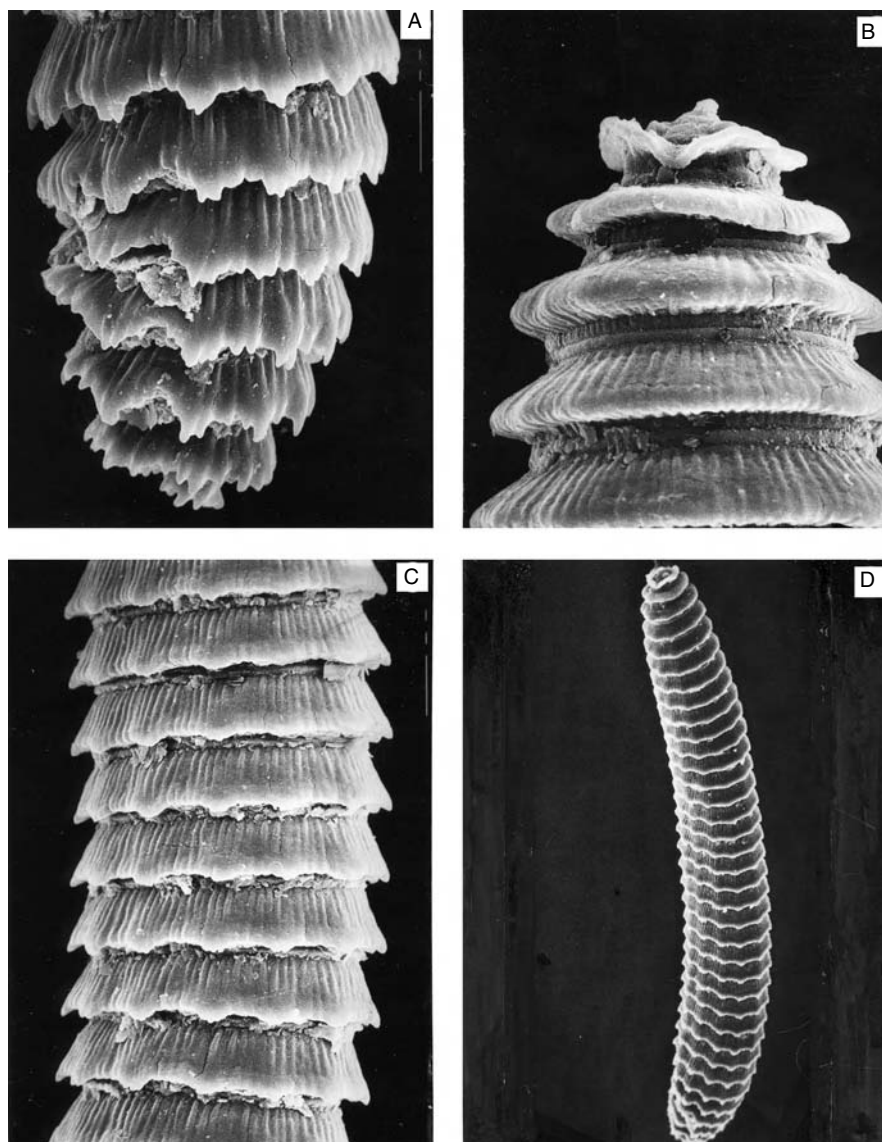
syn. *Criconema* (*Variasquamata* Mehta & Raski, 1971)

*Pseudocriconema* Minagawa, 1984, n. grad.

(Figs 116, 119, J–M)

#### Diagnosis

Genus *Ogma*. Females 0.27–0.86 mm long, with 51–88 annules; **scales unmodified and undivided; annules in extremities not fringed. Submedian lobes present**, may be reduced. Stylet 48–116  $\mu\text{m}$  long. Vulva 10–19 annules from terminus; VL/VB 1.1–2.3. Tail conical. Males usually with three incisures in lateral field. Fourth-stage juvenile with 10–15 rows of scales.



**Fig. 116.** *Ogma (Ogma) serratum* (Khan & Siddiqi) Siddiqi. Scanning electron micrographs of paratype female. A. Tail end. B. Head end. C. Midbody region. D. Entire female.

### Type species

*Ogma (Ogma) murrayi* Southern, 1914

syn. *Hoplolaimus murrayi* (Southern) Menzel, 1917

*Iota murrayi* (Southern) Micoletzky, 1925

*Criconema murrayi* (Southern) Taylor, 1936

*Variasquamata murrayi* (Southern) Khan, Chawla & Saha, 1976

## Other species

- Ogma* (*Ogma*) *andense* Vovlas, Ciancio & Carbonell-Torres, 1991  
*O. (O.) brevistylus* Toida, 1983 (original spelling *brevistylum*)  
*O. (O.) caspametscheri* Van den Berg, Quénéhervé & Tiedt, 1999  
*O. (O.) castellanum* Andrásy, 1985  
*O. (O.) comahuense* Brugni & Chaves, 1994  
*O. (O.) danubiale* Andrásy, 1985  
*O. (O.) decalineatum* (Chitwood, 1957) Andrásy, 1979  
   syn. *Criconema decalineatum* Chitwood, 1957  
     *Variasquamata decalineata* (Chitwood) Khan, Chawla & Saha, 1976  
     *Criconema (Variasquamata) gracile* Mehta & Raski, 1971  
     *Variasquamata gracilis* (Mehta & Raski) Khan, Chawla & Saha, 1976  
     *Ogma gracile* (Mehta & Raski) Ebsary, 1981  
     *Criconema coffeae* Edward, Misra & Rai, 1970  
     *Ogma coffeae* (Edward, Misra & Rai) Andrásy, 1979  
*O. dracomontanum* (Van den Berg, 1983) Siddiqi, 1986  
   syn. *Crossonema dracomontanum* Van den Berg, 1983  
     *Syro dracomontanus* (Van den Berg) Orton Williams, 1985  
*O. (O.) duodevigintilineatum* (Andrásy, 1968) Andrásy, 1979  
   syn. *Criconema duodevigintilineatum* Andrásy, 1968  
     *Variasquamata duodevigintilineata* (Andrásy) Khan, Chawla & Saha, 1976  
*O. (O.) fagini* Escuer & Bello, 1996  
*O. (O.) floridense* Vovlas, Inserra & Esser, 1991  
*O. (O.) fotedari* (Mahajan & Bijral, 1973) Andrásy, 1979  
   syn. *Criconema (Variasquamata) fotedari* Mahajan & Bijral, 1973 (sp. inq. for  
     Khan, Chawla & Saha, 1976)  
*O. (O.) hechuanense* Kaiji & Weisheng, 1991  
*O. (O.) inornatum* (Van den Berg, 1983) Siddiqi, 1986  
   syn. *Crossonema inornatum* Van den Berg, 1983  
*O. (O.) japonicum* (Minagawa, 1984) Siddiqi, 1986  
   syn. *Pseudocriconema japonicum* Minagawa, 1984  
*O. (O.) koesanense* Choi & Geraert, 1994  
*O. (O.) naomiae* Van den Berg, 1992  
*O. (O.) nemorosum* Minagawa, 1993  
*O. (O.) octangulare* (Cobb, 1914) Schuurmans Stekhoven & Teunissen, 1938  
   syn. *Iota octangularis* Cobb, 1914  
     *Hoplolaimus octangularis* (Cobb) Menzel, 1917  
     *Criconema octangulare* (Cobb) Taylor, 1936  
     *Variasquamata octangularis* (Cobb) Khan *et al.*, 1976  
     *Criconema punici* Edward, Misra, Peter & Rai, 1971  
     *Seriespinula punici* (Edward *et al.*) Khan, Chawla & Saha, 1976  
     *Ogma (Ogma) punici* (Edward *et al.*) Siddiqi, 1986  
*O. (O.) ornatum* Mohilal & Dhanachand, 1998 (original spelling *ornama*)  
*O. (O.) ornatum* Van den Berg, 1994  
*O. (O.) parvum* Ahmad, Jairajpuri & Rahmani, 1991  
*O. (O.) rhombosquamatum* (Mehta & Raski, 1971) Andrásy, 1979  
   syn. *Criconema (Variasquamata) rhombosquamatum* Mehta & Raski, 1971

- Variasquamata rhombosquamata* (Mehta & Raski) Khan, Chawla & Saha, 1976
- O. (O.) *sagi* Raski & Valenzuela-A., 1988
- O. (O.) *sassafras* Reay & Davies, 1998  
syn. *Ogma sassafras* Reay & Davies, 1998
- O. (O.) *serratum* (Khan & Siddiqi, 1963) Siddiqi, 1986  
syn. *Criconema serratum* Khan & Siddiqi, 1963  
*Lobocriconema serratum* (Khan & Siddiqi) De Grisse & Loof, 1965  
*Criconemoides serratus* (Khan & Siddiqi) Raski & Golden, 1966  
*Neolobocriconema serratum* (Khan & Siddiqi) Mehta & Raski, 1971  
*Ogma serratum* (Khan & Siddiqi) Raski & Luc, 1987  
*Ogma* (*Homogma*) *serratum* (Khan & Siddiqi, 1963) Siddiqi, 1986  
*Paralobocriconema serratum* (Khan & Siddiqi) Minagawa, 1986  
*Criconema sulcatum* Golden & Friedman, 1964  
*Lobocriconema sulcatum* (Golden & Friedman) De Grisse & Loof, 1965  
*Criconemoides sulcatus* (Golden & Friedman) Raski & Golden, 1966  
*Ogma* (*Homogma*) *sulcatum* (Golden & Friedman) Siddiqi, 1986
- O. (O.) *simlaense* (Jairajpuri, 1963) Andr ssy, 1979  
syn. *Criconema simlaense* Jairajpuri, 1963  
*Variasquamata simlaensis* (Jairajpuri) Khan, Chawla & Saha, 1976  
*Variasquamata rhosimum* Khan, Chawla & Saha, 1976  
*Ogma rhosimum* (Khan *et al.*) Andr ssy, 1979  
*Ogma goldeni* Handoo, 1983
- O. (O.) *spinosum* Andr ssy, 1979
- O. (O.) *squamiferum* (Heyns, 1970) Andr ssy, 1979  
syn. *Lobocriconema squamiferum* Heyns, 1970  
*Criconema squamiferum* (Heyns) Loof & De Grisse, 1974
- O. (O.) *terrestris* Raski & Valenzuela-A., 1986
- O. (O.) *tokobaevi* (Gritsenko, 1979) Kapoor, 1983  
syn. *Criconema* (*Variasquamata*) *tokobaevi* Gritsenko, 1979  
*Ogma tokobaevi* (Gritsenko) Raski & Luc, 1987
- O. (O.) *toparti* Van den Berg & Qu  n  herv , 1995
- O. (O.) *trigonolepidum* Minagawa, 1988
- O. (O.) *tuberculatum* Van den Berg, 1996
- O. (O.) *ueckermanni* Van den Berg, 1992
- O. (O.) *zernovi* Kirjanova, 1948  
syn. *Criconema zernovi* (Kirjanova) Chitwood, 1957  
*Variasquamata zernovi* (Kirjanova) Khan, Chawla & Saha, 1976

### Species inquirendae

- Ogma boettgeri* (Meyl, 1954) Raski & Luc, 1987  
syn. *Criconemoides boettgeri* Meyl, 1954  
*Criconema boettgeri* (Meyl, 1954) De Grisse & Loof, 1965
- Ogma minutum* Kirjanova, 1948  
syn. *Criconema minutum* (Kirjanova) Chitwood, 1957
- Ogma multiannulatum* Shahina & Maqbool, 1991
- Ogma qamari* Shahina & Maqbool, 1991

- Ogma sadabhari* Shahina & Maqbool, 1991  
*Ogma spasskii* (Nesterov & Lisetskaya) Andrásy, 1979  
 syn. *Criconema spasskii* Nesterov & Lisetskaya, 1965  
*Ogma triconodon* Schuurmans Stekhoven & Teunissen, 1938  
 syn. *Criconema triconodon* (Schuurmans Stekhoven & Teunissen) de Coninck,  
 1943

#### Note

Shahina & Maqbool (1991) described three new species of *Ogma* from Karachi, Pakistan, viz. *O. sadabhari*, *O. multiannulata* and *O. qamari*. These species are very similar to juveniles of *Hemicriconemoides mangiferae* and some *Criconema* spp. The photographs of the posteriors of females showing the vulva given by these authors are judged to be of different species. These three species are proposed here as *species inquirendae* needing further study to decide their identity and systematic position.

ETYMOLOGY. From Greek *ogmos* = a furrow or *ogmeuein* = slowly move forward. *Ogma* is a Greek word, not a latinized one. If a Greek word ends in *-ma* (e.g. *-nema*, *-derma*), it is neuter in gender.

The type species was found in moss from Belclare, County Mayo, Ireland. Species of *Ogma* (*Ogma*) are known from Asia (*O. coffeae*, *O. decalineatum*, *O. fotedari*, *O. hechuanense*, *O. koesanense*, *O. octangulare*, *O. parvum*, *O. rhombosquamatum*, *O. simlaense*, *O. spinosum*, *O. trigonolepidum* and *O. tokobaevi*), Europe (*O. fagini*, *O. murrayi*, *O. octangulare*, *O. rhombosquamatum* and *O. zernovi*), North America (*O. decalineatum*, *O. murrayi*, *O. octangulare*), South America (*O. decalineatum*, *O. duodevigintilineatum*, *O. toparti*) and Africa (*O. decalineatum*, *O. octangulare*, *O. squamiferum*, *O. tuberculatum*). A key to *Ogma* spp. was given by Minagawa (1988a).

#### Subgenus *Seriespinula* Mehta & Raski, 1971

syn. *Crossonema* (*Seriespinula* Mehta & Raski, 1971)

(Fig. 117, A–C)

#### Diagnosis

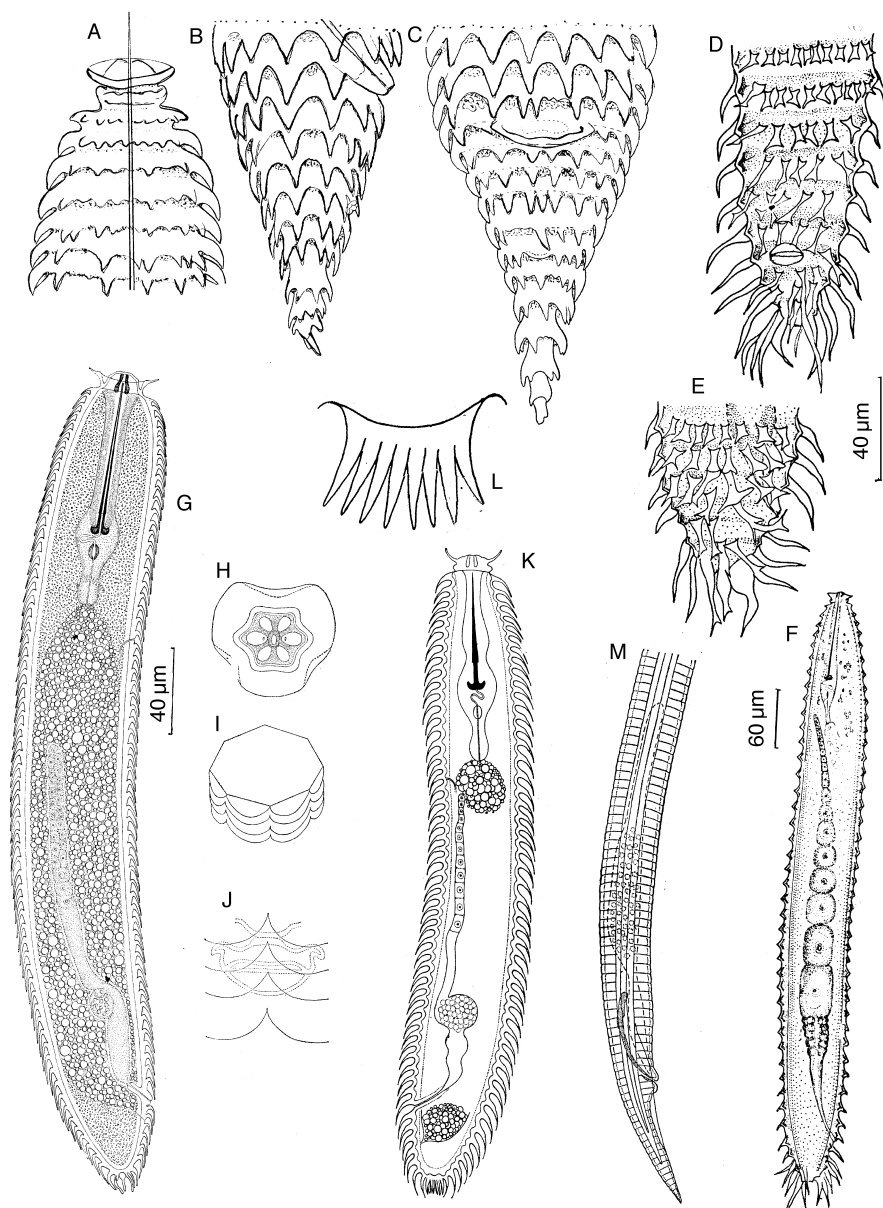
Genus *Ogma*. Females about 0.3–0.6 mm long and with 50–90 annules; annules on extremities often fringed (not in type species of the subgenus). Scales arranged in 8–20 longitudinal rows, **usually divided into two to five spine-like processes**. Cephalic region with two annules, anterior one discoidal. **Submedian lobes usually absent**. Stylet 49–125 µm long. Vulva 6–15 annules from terminus; VL/VB 1.5–2.3. **Tail conical, pointed**. Fourth-stage juveniles with 11–13 rows of scales tipped with a single spine.

#### Type species

*Seriespinula cobbi* (Micoletzky, 1925) Mehta & Raski, 1971

#### Present status

*Ogma* (*Seriespinula*) *cobbi* (Micoletzky) Siddiqi, 1986  
 syn. *Iota cobbi* Micoletzky, 1925



**Fig. 117.** A–C. *Ogma (Seriespinula) cobbi* (Micoletzky). D–F. *Crosssonema taylatum* Khan, Chawla & Saha. G–J. *Ogma (Pateracphalanema) imbricatum* (Colbran). K–M. *Ogma (P) pectinatum* (Colbran). M. Male, remainder females. A. Head end. B–E and M. Tail ends. F, G and K. Entire females. H. En face view. I. Transverse section in midbody region. J. Vulva in ventral view. L. Distal portion of scale in midbody region. (A–C. Redrawn after Micoletzky (1925). D–F. After Khan *et al.* (1976). G–M. After Colbran (1962, 1965), courtesy Queensland Journal of Agricultural and Animal Sciences.)

- Criconema cobbi* (Micoletzky) Taylor, 1936  
*Criconema cobbi duplex* de Coninck, 1945  
*Criconema cobbi multiplex* de Coninck, 1945  
*C. cobbi cobbi* (Micoletzky) Taylor, 1936 (= *C. cobbi typica* de Coninck, 1945)  
*C. (Seriespinula) cobbi* (Micoletzky) Mehta & Raski, 1971  
*Seriespinula cobbi* (Micoletzky) Mehta & Raski, 1971  
*Crossonema (Seriespinula) cobbi* (Micoletzky) Mehta & Raski, 1971  
*Criconema schuurmansstekhoveni* de Coninck, 1943

#### Other species

- Ogma (Seriespinula) allieri* (Doucet, 1981) Siddiqi, 1986  
 syn. *Seriespinula allieri* Doucet, 1981  
*Ogma allieri* (Doucet) Raski & Luc, 1987  
*O. (S.) alternatum* (Doucet, 1986) Raski & Luc, 1987  
 syn. *Seriespinula alternata* Doucet, 1986  
*Ogma alternatum* (Doucet) Raski & Luc, 1987  
*O. (S.) andrassyi* Reay & Davies, 1998 (was nom. nov.)  
 syn. *Seriespinula australis* Andr ssy, 1986  
*Ogma australe* (Andr ssy, 1986) Ebsary, 1991, nec *Ogma australe* (Colbran, 1963) Siddiqi, 1986  
*O. (S.) cactus* (Andr ssy, 1979) Siddiqi, 1986  
 syn. *Seriespinula cactus* Andr ssy, 1979  
*Blandicephalanema cactus* (Andr ssy) Ebsary, 1981  
*O. (S.) feckneri* Reay & Davies, 1998  
 syn. *Ogma feckneri* Reay & Davies, 1998  
*Seriespinula feckneri* (Reay & Davies) comb. n.  
*O. (S.) hungaricum* (Andr ssy, 1962) Siddiqi, 1986  
 syn. *Criconema hungaricum* Andr ssy, 1962  
*Crossonema (Seriespinula) hungaricum* (Andr ssy) Mehta & Raski, 1971  
*O. (S.) octozonale* (Momota & Ohshima, 1974) Siddiqi, 1986  
 syn. *Crossonema (Seriespinula) octozonale* Momota & Ohshima, 1974  
*Seriespinula octozanalis* Momota and Ohshima, 1974  
*Seriespinula octozonalis* (Momota & Ohshima) Khan, Chawla & Saha, 1976  
*Seriespinula sokliensis* Choi & Geraert, 1975  
*Ogma sokliense* (Choi & Geraert) Siddiqi, 1986  
*O. (S.) racemispinosum* (Mehta, Raski & Valenzuela, 1982) Siddiqi, 1986  
 syn. *Seriespinula racemispinosa* Mehta, Raski & Valenzuela, 1982  
*O. (S.) seymouri* (Wu, 1965) Siddiqi, 1986  
 syn. *Criconema seymouri* Wu, 1965  
*Crossonema (Seriespinula) seymouri* (Wu) Mehta & Raski, 1971  
*Seriespinula seymouri* (Wu) Mehta & Raski, 1971  
*Seriespinula seymouri* (Wu) Khan, Chawla & Saha, 1976  
*O. (S.) tenuicaudatum* (Siddiqi, 1961) Siddiqi, 1986  
 syn. *Criconema tenuicaudatum* Siddiqi, 1961  
*Crossonema (Seriespinula) tenuicaudatum* (Siddiqi) Mehta & Raski, 1971  
*Seriespinula tenuicaudata* (Siddiqi) Mehta & Raski, 1971



- Seriespinula tenuicaudata* (Siddiqi) Khan, Chawla & Saha, 1976  
*Seriespinula impar* Khan, Chawla & Saha, 1976  
*Ogma* (*Seriespinula*) *impar* (Khan, Chawla & Saha) Siddiqi, 1986  
*O. (S.) venustum* (Mehta & Raski, 1971) Siddiqi, 1986  
 syn. *Crossonema* (*Seriespinula*) *venustum* Mehta & Raski, 1971  
*Seriespinula venusta* (Mehta & Raski) Mehta & Raski, 1971

#### Remark

The subgenus *Seriespinula* differs from the subgenus *Ogma* in having the anterior and posterior ends usually with fringes of spines, body scales usually with two to five finger-like projections and the absence of submedian lobes.

ETYMOLOGY. Latin *series* = row, and *spinula* = Latin diminutive of spine.

The type species occurs widely in Europe and is also found in the USA. It was originally described from sphagnum (bog moss) from Gribsee-Moor, Denmark.

#### Subgenus *Macrocriconema* Minagawa, 1986, grad. n.

(Fig. 118)

#### Diagnosis

Genus *Ogma*. Females 0.5–0.7 mm long, with 50–65 annules bearing scales arranged in up to 18 longitudinal rows in type species, each scale rectangular and membranous and has a scale-like appendage. Cephalic region with two annules, not bearing scales; anterior annule discoidal. **Submedian lobes prominent.** Stylet 49–125  $\mu\text{m}$  long. Vulva closed, at fifth or sixth annule from terminus in type species; VL/VB about 1.5. Tail end conoid-rounded. Fourth-stage juveniles with 11–15 rows of membranous scales varying in length and shape. Male not known.

#### Type species

*Macrocriconema querci* (Choi & Geraert, 1975) Minagawa, 1986

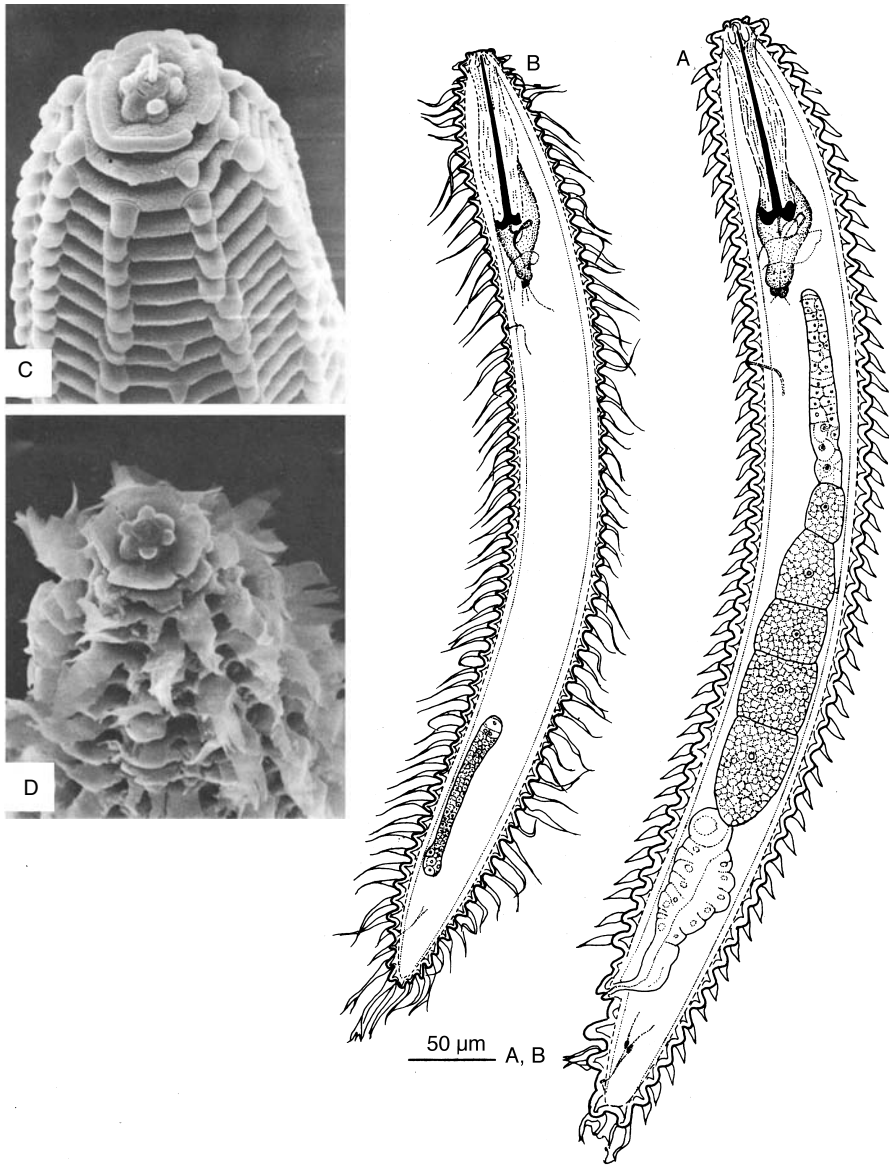
#### Present status

- Ogma* (*Macrocriconema*) *querci* (Choi & Geraert, 1975) Andr ssy, 1979  
 syn. *Criconema* (*Variasquamata*) *querci* Choi & Geraert, 1975  
*Crossonema querci* (Choi & Geraert) Ebsary, 1981  
*Ogma querci* (Choi & Geraert) Andr ssy, 1979  
*Macrocriconema querci* (Choi & Geraert) Minagawa, 1986

No other species.

ETYMOLOGY. From *macros* = large (for body and stylet), and *Criconema*.

The type species was described from soil around roots of *Quercus acutissima* in Nam Do, Korea. It is also found associated with mulberry, *Acer sieboldianum*, *Prunus jamasakura*, *Rubus palmatus*, *Styrax japonica*, *Fraxinus longicuspis* and *Orixa japonica* in Japan (Minagawa, 1986).



**Fig. 118.** *Ogmia* (*Macrocriconema*) *querci* (Choi & Geraert) Andr ssy. A. Female. B. Fourth-stage juvenile. C and D. Scanning electron micrographs of anterior ends of female and fourth-stage juvenile, respectively. (After Minagawa (1986), courtesy National Institute of Agro-Environmental Sciences, Japan.)

**Subgenus *Pateracephalanema* Mehta & Raski, 1971****syn. *Syro* Orton Williams, 1985*****Pellipecten* Siddiqi, 1986**

(Fig. 117, G–M)

**Diagnosis**

Genus *Ogma*. Body 0.5 mm or less long, with about 55–98 strongly retrorse annules. **Annules with 8–16 round, laterally contiguous scales, which may be smooth, crenate or comb-like**, lying in longitudinal rows over the body and closely adpressed to it. **Cephalic region offset, with one large, saucer-shaped smooth annule**; submedian lobes absent. Stylet 50–90  $\mu$ m long. Vulva on seventh to ninth annule from terminus. VL/VB 0.6–1.2. **Tail end obtusely rounded**. Male with round, continuous, striated cephalic region, four incisures in lateral field, setose, arcuate spicules and a low, subterminal bursa.

**Type species***Pateracephalanema imbricatum* (Colbran, 1965) Mehta & Raski, 1971**Present status***Ogma* (*Pateracephalanema*) *imbricatum* (Colbran, 1965) Siddiqi, 1986syn. *Criconema imbricatum* Colbran, 1965*Pateracephalanema imbricatum* (Colbran) Mehta & Raski, 1971**Other species***Ogma* (*Pateracephalanema*) *alticolum* (Colbran, 1965) Siddiqi, 1986syn. *Criconema alticolum* Colbran, 1965*Pateracephalanema alticolum* (Colbran) Mehta & Raski, 1971*O. (P.) australe* (Colbran, 1963) Siddiqi, 1986syn. *Criconema australe* Colbran, 1963*Pateracephalanema australe* (Colbran) Mehta & Raski, 1971*Ogma australe* (Colbran) Reay & Davies, 1998*O. (P.) hughdavidi* (Orton Williams, 1985) Raski & Luc, 1987syn. *Syro hughdavidi* Orton Williams, 1985*Ogma hughdavidi* (Orton Williams) Raski & Luc, 1987*Pateracephalanema hughdavidi* (Orton Williams) comb. n.*O. (P.) melanesicum* (Andrássy, 1979) Siddiqi, 1986syn. *Seriespinula melanesicum* Andr  ssy, 1979*Crossonema melanesicum* (Andr  ssy) Ebsary, 1981*Syro melanesicus* (Andr  ssy) Orton Williams, 1985*Ogma (Seriespinula) melanesicum* (Andr  ssy, 1979) Siddiqi, 1986*Pateracephalanema melanesicum* (Andr  ssy) comb. n.*O. (P.) pectinatum* (Colbran, 1962) Siddiqi, 1986syn. *Criconema pectinatum* Colbran, 1962*Pateracephalanema pectinatum* (Colbran) Mehta & Raski, 1971*Ogma (Pellipecten) pectinatum* (Colbran) Siddiqi, 1986*Ogma pectinatum* (Colbran) Reay & Davies, 1998*Pellipecten pectinatus* (Colbran) Siddiqi, 1986

- O. (P.) pellitum* (Andrássy, 1979) Siddiqi, 1986  
 syn. *Pateracephalanema pellitum* Andrássy, 1979  
     *Ogma (Pellipecten) pellitum* (Andrássy) Siddiqi, 1986  
     *Ogma pellitum* (Andrássy) Reay & Davies, 1998  
     *Pellipecten pellitus* (Andrássy) Siddiqi, 1986
- O. (P.) vexillatrix* (Orton Williams, 1985) Raski & Luc, 1987  
 syn. *Syro vexillatrix* Orton Williams, 1985  
     *Ogma vexillatrix* (Orton Williams, 1985) Raski & Luc, 1987  
     *Pateracephalanema vexillatrix* (Orton Williams, 1985) comb. n.

#### Note

In having one large saucer-shaped head annule and rounded tail end, *Syro* resembles *Pateracephalanema* but differs from it in having fringed cephalic annules and scales appearing comb-like. These differences are not sufficient to recognize *Syro* as distinct from *Pateracephalanema*.

ETYMOLOGY. From the Latin *patera* = flat dish, and Greek *kephalé* = head (for dish-like head annule), and *nema* = nematode.

*Ogma (Pateracephalanema) imbricatum* was found in sandy soil dominated by *Eucalyptus pilularis* in Queensland, Australia (Colbran, 1965). *Ogma (Pateracephalanema) vexillatrix* was found in rhizosphere soil of *Crotalaria lunata* (Sabaceae), at Tobua, Nembi Plateau, Southern Highlands, New Guinea. *Ogma (Pateracephalanema) melanesicum* was found in rainforest soil at Macaranga, New Britain. Other species are indigenous to Australia.

#### Subgenus *Orphreyus* subgen. n.

(Fig. 115, I–L)

#### Diagnosis

Genus *Ogma*. Females 0.28 mm long, with 39 annules bearing elongate, spine-like appendages bi- or trifurcate at tip in type species. **Size and arrangement of appendages different in dorsal and ventral sectors of annules.** On most of body, appendages longer on ventral than dorsal sector and, in type species, form a continuous complete fringe or only dorsal sector with a fringe (ventral sector smooth, lacking appendages) in an alternating arrangement. **Cephalic region of one saucer-shaped annule wider than adjacent body annule.** Submedian lobes absent. Stylet 72  $\mu$ m long in type species. Vulva closed, three to four annules from terminus; lips conoid, projecting beyond body contour; VL/VB = <1. Posterior extremity conoid-rounded; cuticular appendages projecting well beyond body contour. Male and juveniles not known.

#### Type species

*Orphreyus orphreyifer* (Orton Williams, 1985) comb. n.

## Present status

- Ogma* (*Orphreyus*) *orphreyifer* (Orton Williams, 1985) comb. n.  
 syn. *Syro orphreyifer* Orton Williams, 1985  
*Orphreyus orphreyifer* (Orton Williams) comb. n.

## Other species

- Ogma* (*Orphreyus*) *lentiforme* Schuurmans Stekhoven & Teunissen, 1938  
 syn. *Ogma lentiforme* Schuurmans Stekhoven & Teunissen, 1938  
*Criconema lentiforme* (Schuurmans Stekhoven & Teunissen) de Coninck, 1943  
*Criconema* (*Variasquamata*) *lentiforme* (Schuurmans Stekhoven & Teunissen) Mehta & Raski, 1971  
*Variasquamata lentiformis* (Schuurmans Stekhoven & Teunissen) Khan, Chawla & Saha, 1976  
*Orphreyus lentiformis* (Schuurmans Stekhoven & Teunissen, 1938) comb. n.  
*Ogma tripus* Schuurmans Stekhoven & Teunissen, 1938  
*Criconema tripus* (Schuurmans Stekhoven & Teunissen) de Coninck, 1945  
*Orphreyus tripus* (Schuurmans Stekhoven & Teunissen) comb. n.  
*O.* (*Orphreyus*) *nyalaziense* Van den Berg, 1991  
 syn. *Ogma nyalaziense* Van den Berg, 1991  
*Orphreyus nyalaziensis* (Van den Berg) comb. n.

ETYMOLOGY. From orphrey, a late Middle English word for a richly decorated band on a garment.

The type species was found in the rhizosphere of sweet potato, *Ipomoea batatas* at Kuari Kogu, Tari, Southern Highlands, New Guinea.

**Subgenus *Croserinema* Khan, Chawla & Saha, 1976 (Siddiqi, 1986)**

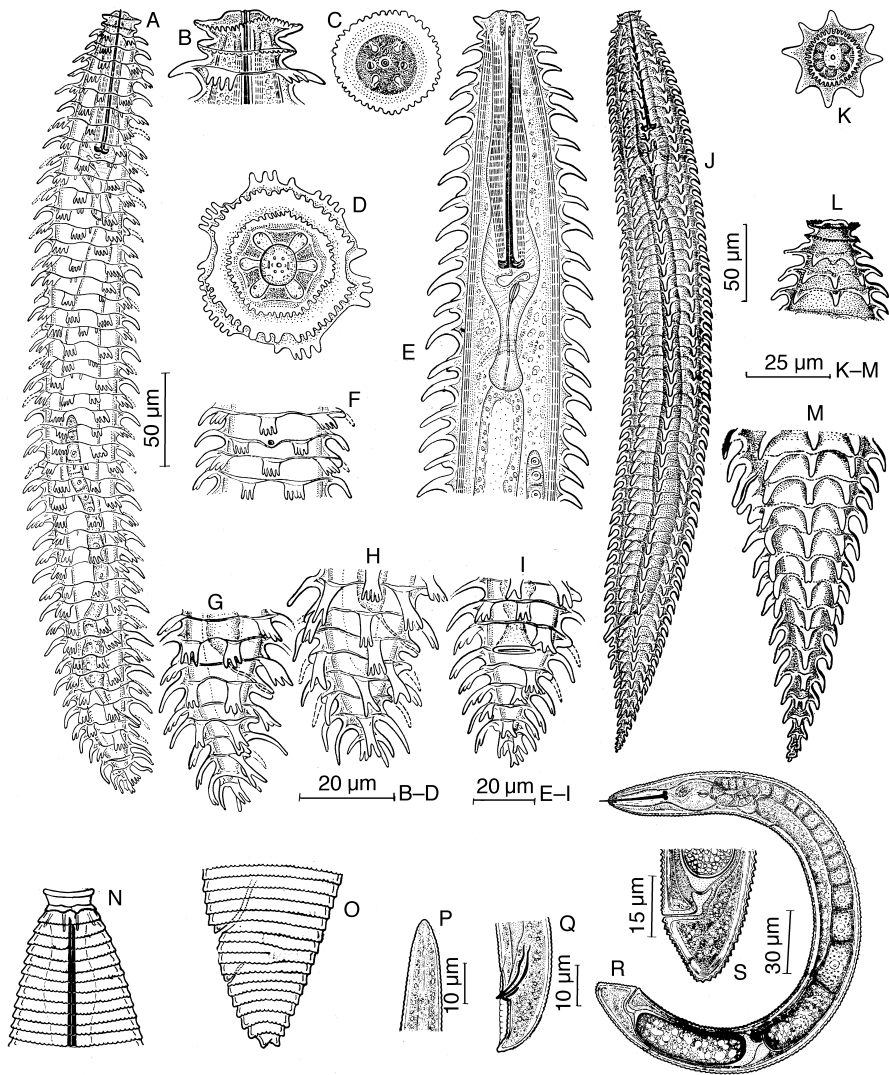
(Fig. 119, A–I)

## Diagnosis

Genus *Ogma*. Body with 45–60 annules, **each annule bearing eight palmate scales which alternate with those on adjacent annules**; each palmate scale has two to six (usually four to five) finger-like spines; single spines may occur between these scales. Cephalic region with two annules, anterior one wider than posterior, both having fringed margins. Six pseudolips and submedian lobes present. Stylet 67–103  $\mu\text{m}$  long in type species. Vulva closed, lips conical, conspicuously withdrawn from body contour, on fourth to seventh annule from terminus. Postvulval body part conoid-rounded. Male not known. Juveniles with palmate scales and simple spines, more numerous than in females.

## Type species

*Croserinema palmatum* (Siddiqi & Southey, 1962) Khan, Chawla & Saha, 1976



**Fig. 119.** A–I. *Ogma* (*Croserinema*) *palmatum* (Siddiqi & Southey). J–M. *Ogma* (*Ogma*) *murrayi* (Southern). N and O. *Discocriconemella limitanea* (Luc). P–S. *Criconemoides* (*Criconemella*) *parvulus* Siddiqi. A, J and R. Females. B, L and N. Female head ends. C. Cross-section through female second head annule. D and K. *En face* views of females. E. Female oesophageal region. F. Palmate scales at midbody. G–I, M, O and S. Female tail ends. P and Q. Male head and tail end, respectively. (A–I. After Siddiqi & Southey (1962). J–M. After Siddiqi (1965). N and O. After Luc (1959). P–S. After Siddiqi (1961a). A–O. Courtesy *Nematologica*. P–S. Courtesy Helminthological Society of Washington.)

## Present status

- Ogma* (*Croserinema*) *palmatum* (Siddiqi & Southey, 1962) Siddiqi, 1986  
 syn. *Criconema palmatum* Siddiqi & Southey, 1962  
*Crossonema* (*Crossonema*) *palmatum* (Siddiqi & Southey) Mehta & Raski,  
 1971.  
*Croserinema palmatum* (Siddiqi & Southey) Khan, Chawla & Saha, 1976  
 No other species.

## Remarks

*Croserinema* was proposed by Khan *et al.* (1976) to accommodate *Criconema palmatum* Siddiqi & Southey, 1962. Andr  ssy (1979) recognized the genus on the basis of the palmate appendages arranged on the body in alternating rows, a unique adult feature for Criconematinae. Ebsary (1981) synonymized *Croserinema* with *Crossonema* because he found similar appendages in posterior region of *Crossonema civellae*. However, the configuration of the posterior region as compared to that over most of the body is often very variable and cannot be given too much taxonomic importance.

ETYMOLOGY. *Croseri* derived from first letters of names *Crossonema* and *Seriespinula*, and *nema* = nematode.

The type species occurs widely in Belgium, Italy, the UK and the USA. It was originally described from strawberry soil in Devon, UK.

**Genus *Crossonema* Mehta & Raski, 1971**

syn. ***Neocrossonema* Ebsary, 1981**

***Homogma* Siddiqi, 1986**

***Ogma* (*Homogma* Siddiqi, 1986)**

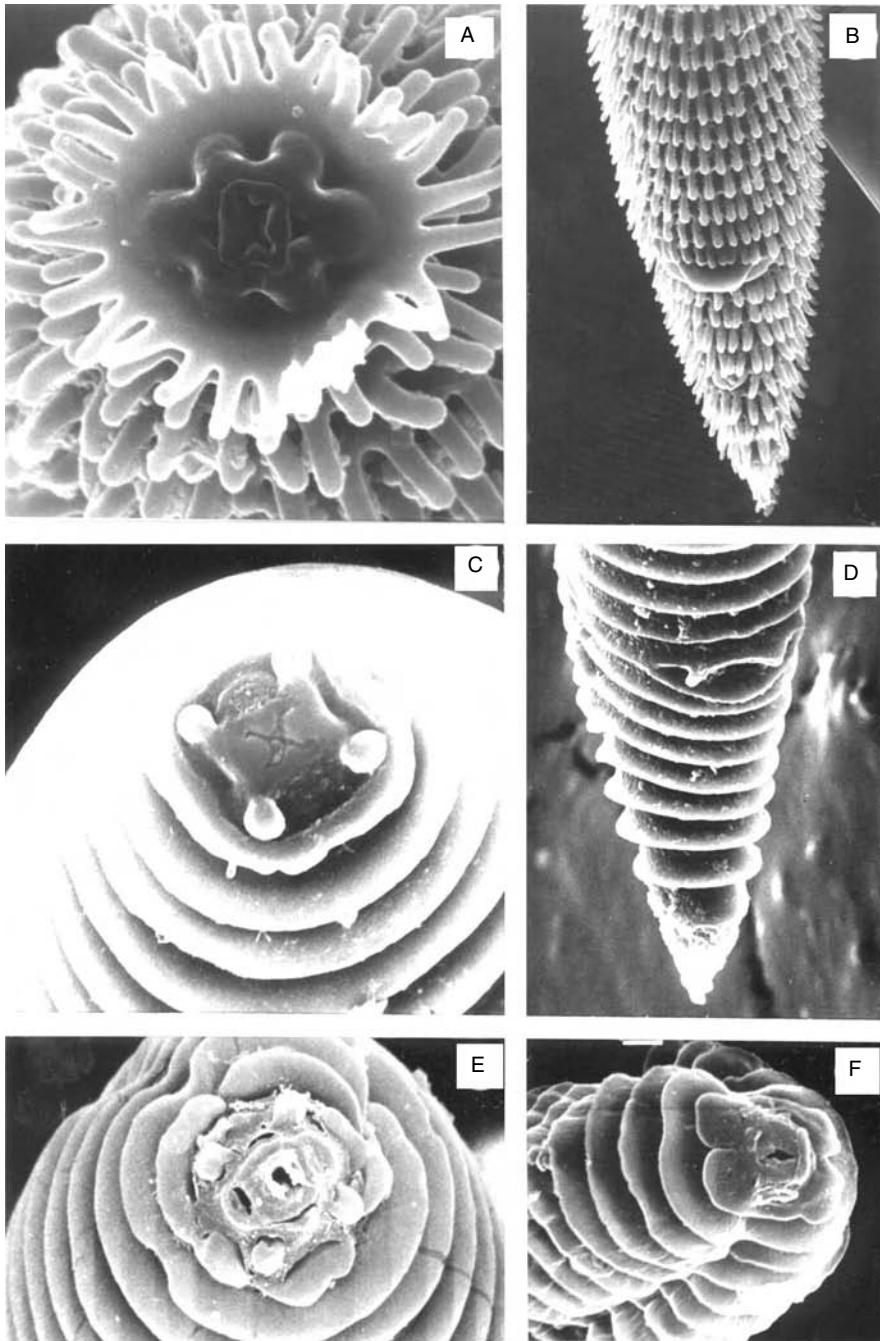
(Fig. 114, B–D; 120(a)A & B)

## Diagnosis

Genus *Ogma*. Females 0.29–0.86 mm, with 40–93 annules. **Annules round, not lobed, with a continuous fringe of fine or blunt spines on most of body; spines simple, but some in posterior region modified in being bifurcate, knobbed or clubbed.** Cephalic region offset, with two differentiated annules; anterior cephalic annule smooth, crenate or spined. Lip areas elevated, submedian lobes absent. Stylet 62–125  $\mu\text{m}$  long. Vulva 3–16 annules from terminus, lips generally pointed. VL/VB about 0.8–1.1. Tail conoid-rounded or conoid pointed. Males with three, sometimes four incisures in lateral field, low bursa and setose spicules. Fourth-stage juveniles with longitudinal rows of broad scales, each bearing one or more spines.

## Type species

- Crossonema civellae* (Steiner, 1949) Mehta & Raski, 1971  
 syn. *Criconema civellae* Steiner, 1949  
*Ogma civellae* (Steiner) Raski & Luc, 1987  
*Ogma civellae civellae* (Steiner, 1949) Raski & Luc, 1987 (Reay & Davies,  
 1998)



**Fig. 120(a).** Scanning electron micrographs. A and B. *Crossonema capitospinosum* Ebsary, female head (*en face*) and tail end (ventral view showing spines and vulval lips), respectively. C and D. *Macroposthonia parareedi* Ebsary, female head (*en face*) and tail end showing vulval lips, respectively. E. *Macroposthonia xenoplax* (Raski), female head (*en face*). F. *Criconemoides (Criconemella) parvus* Raski, anterior end of female. (A–D. After Ebsary (1981), courtesy *Canadian Journal of Zoology*. F. Courtesy P.A.A. Loof.)



- Criconema celetum* Wu, 1960  
*Crossonema* (*Crossonema*) *celetum* (Wu) Siddiqi, 1986  
*Criconema eury soma* Golden & Friedman, 1964  
*Crossonema* (*Crossonema*) *eury soma* (Golden & Friedman) Siddiqi, 1986  
*Criconema vishwanathum* Edward & Misra, 1966  
*Crossonema* (*Crossonema*) *vishwanathum* (Edward & Misra) Siddiqi, 1986

### Other species

- Crossonema abies* Andr ssy, 1979  
 syn. *Neocrossonema abies* (Andr ssy) Ebsary, 1981  
*Ogma abies* (Andr ssy) Raski & Luc, 1987  
*C. aquitanense* (Fies, 1968) Mehta & Raski, 1971  
 syn. *Criconema aquitanense* Fies, 1968  
*Crossonema* (*Crossonema*) *aquitanense* (Fies) Mehta & Raski, 1971  
*Neocrossonema aquitanense* (Fies) Ebsary, 1981  
*Crossonema aquitanense* (Fies) Khan, Chawla & Saha, 1976  
*Ogma aquitanense* (Fies) Raski & Luc, 1987  
*C. arboreum* (Reay & Davies, 1998) comb. n.  
 syn. *Ogma civellae arboreum* Reay & Davies, 1998  
*C. bellum* (Reay & Davies, 1998) comb. n.  
 syn. *Ogma bellum* Reay & Davies, 1998  
*C. capitospinosum* Ebsary, 1979  
 syn. *Neocrossonema capitospinosum* (Ebsary) Ebsary, 1981  
*Ogma capitospinosum* (Ebsary) Raski & Luc, 1987  
*C. centone* Eroshenko, 1980  
 syn. *Ogma centone* (Eroshenko) Raski & Luc, 1987  
*C. centurian* Bajaj, 1998  
*C. chrisbarnardi* (Heyns, 1970) Loof & De Grisse, 1974  
 syn. *Criconema chrisbarnardi* Heyns, 1970  
*Ogma chrisbarnardi* (Heyns) Andr ssy, 1979  
*Syro chrisbarnardi* (Heyns) Orton Williams, 1985  
*C. coronatum* (Schuurmans Stekhoven & Teunissen, 1938) Mehta & Raski, 1971  
 syn. *Ogma coronatum* Schuurmans Stekhoven & Teunissen, 1938  
*Criconema coronatum* (Schuurmans Stekhoven & Teunissen) de Coninck, 1943  
*Crossonema* (*Crossonema*) *coronatum* (Schuurmans Stekhoven & Teunissen) Mehta & Raski, 1971  
*Seriespinula coronata* (Schuurmans Stekhoven & Teunissen) Andr ssy, 1979  
*Syro coronatus* (Schuurmans Stekhoven & Teunissen) Orton Williams, 1985  
*C. dryum* Minagawa, 1979  
 syn. *Ogma dryum* (Minagawa) Raski & Luc, 1987  
*C. fimbriatum* (Cobb in Taylor, 1936) Mehta & Raski, 1971  
 syn. *Criconema fimbriatum* Cobb in Taylor, 1936  
*Crossonema fimbriatum* (Cobb in Taylor) Khan, Chawla & Saha, 1976  
*Neocrossonema fimbriatum* (Cobb in Taylor) Ebsary, 1981  
*Ogma fimbriatum* (Cobb in Taylor) Raski & Luc, 1987  
*C. fimeivatum* Khan, Chawla & Saha, 1976

- syn. *Ogma fimeivatum* (Khan, Chawla & Saha) Raski & Luc, 1987
- C. haguei* (Reay & Davies, 1998) comb. n.  
syn. *Ogma haguei* Reay & Davies, 1998
- C. horridum* Eroshenko, 1980  
syn. *Ogma horridum* (Eroshenko) Raski & Luc, 1987
- C. latens* Mehta & Raski, 1971  
syn. *Crossonema* (*Crossonema*) *latens* Mehta & Raski, 1971  
*Crossonema latens* (Mehta & Raski) Khan, Chawla & Saha, 1976  
*Ogma latens* (Mehta & Raski) Raski & Luc, 1987
- C. louisi* (Van den Berg, 1991) comb. n.  
syn. *Ogma louisi* Van den Berg, 1991
- C. malabaricum* Muthukrishnan, 1987
- C. menzeli* (Stefanski, 1924) Mehta & Raski, 1971  
syn. *Hoplolaimus menzeli* Stefanski, 1924  
*Iota menzeli* (Stefanski) Micoletzky, 1925  
*Criconema menzeli* (Stefanski) Taylor, 1936  
*Ogma menzeli* (Stefanski) Schuurmans Stekhoven & Teunissen, 1938  
*Crossonema* (*Crossonema*) *menzeli* (Stefanski) Mehta & Raski, 1971  
*Crossonema menzeli* (Stefanski) Khan, Chawla & Saha, 1976  
*Neocrossonema menzeli* (Stefanski) Ebsary, 1981  
*Iota aculeata* Schneider, 1939  
*Criconema aculeatum* (Schneider) de Coninck, 1943  
*Crossonema* (*Crossonema*) *aculeatum* (Schneider) Mehta & Raski, 1971  
*Crossonema aculeatum* (Schneider) Khan, Chawla & Saha, 1976
- C. multisquamatum* (Kirjanova, 1948) Mehta & Raski, 1971  
syn. *Ogma multisquamatum* Kirjanova, 1948  
*Criconema multisquamatum* (Kirjanova) Chitwood, 1957  
*Crossonema* (*Crossonema*) *multisquamatum* (Kirjanova) Mehta & Raski, 1971  
*Crossonema multisquamatum* (Kirjanova) Khan, Chawla & Saha, 1976
- C. nepalense* (Khan, Singh & Lal, 1998) comb. n.  
syn. *Criconema nepalense* Khan, Singh & Lal, 1998
- C. paracivellae* (Decraemer & Geraert, 1992) comb. n.  
syn. *Ogma paracivellae* Decraemer & Geraert, 1992
- C. proclive* (Hoffmann, 1973) Khan, Chawla & Saha, 1976  
syn. *Criconema proclive* Hoffmann, 1973  
*Crossonema proclive* (Hoffmann) Andr  ssy, 1979  
*Neocrossonema proclive* (Hoffmann) Ebsary, 1981  
*Ogma proclive* (Hoffmann) Raski & Luc, 1987
- C. raskii* Rahmani, Jairajpuri & Ahmad, 1985  
syn. *Ogma raskii* (Rahmani, Jairajpuri & Ahmad) Raski & Luc, 1987
- C. taylatum* Khan, Chawla & Saha, 1976  
syn. *Homogma taylatum* (Khan, Chawla & Saha, 1976) Siddiqi, 1986  
*Ogma* (*Homogma*) *taylatum* (Khan, Chawla & Saha) Siddiqi, 1986
- C. taylori* (Jairajpuri, 1964) Mehta & Raski, 1971  
syn. *Criconema taylori* Jairajpuri, 1964  
*Crossonema* (*Crossonema*) *taylori* (Jairajpuri) Mehta & Raski, 1971  
*Crossonema taylori* (Jairajpuri) Khan, Chawla & Saha, 1976

- Ogma taylori* (Jairajpuri, 1964) Siddiqi, 1986  
*C. velutina* Eroshenko, 1980  
 syn. *Ogma velutinum* (Eroshenko) Siddiqi in Raski & Luc (1987)  
*C. villiferum* Eroshenko, 1980  
 syn. *Ogma villiferum* (Eroshenko) Raski & Luc, 1987  
*C. whianum* (Reay & Davies, 1998) comb. n.  
 syn. *Ogma civellae whianum* Reay & Davies, 1998

### Species inquirenda

- Criconema georgiense* Kirjanova, 1958  
 syn. *Crossonema georgiense* (Kirjanova) Ivanova, 1976  
*Ogma georgiense* (Kirjanova) Raski & Luc, 1987

### Remarks

Khan *et al.* (1976) raised the subgenus *Crossonema* to generic rank, proposing a number of new combinations. *Crossonema* as a genus and its new combinations were already proposed by Mehta & Raski (1971). Andr ssy (1979) synonymized *Criconema civellae* with *Criconema multisquamatum* Kirjanova, 1948.)

ETYMOLOGY. From Greek *krossos* = fringe, and *nema* = nematode.

The type species was found feeding on the roots of *Citrus grandis* (L.) Osbeck in a glasshouse at Beltsville, Maryland, USA. It occurs in many countries.

### Genus *Blandicephalanema* Mehta & Raski, 1971

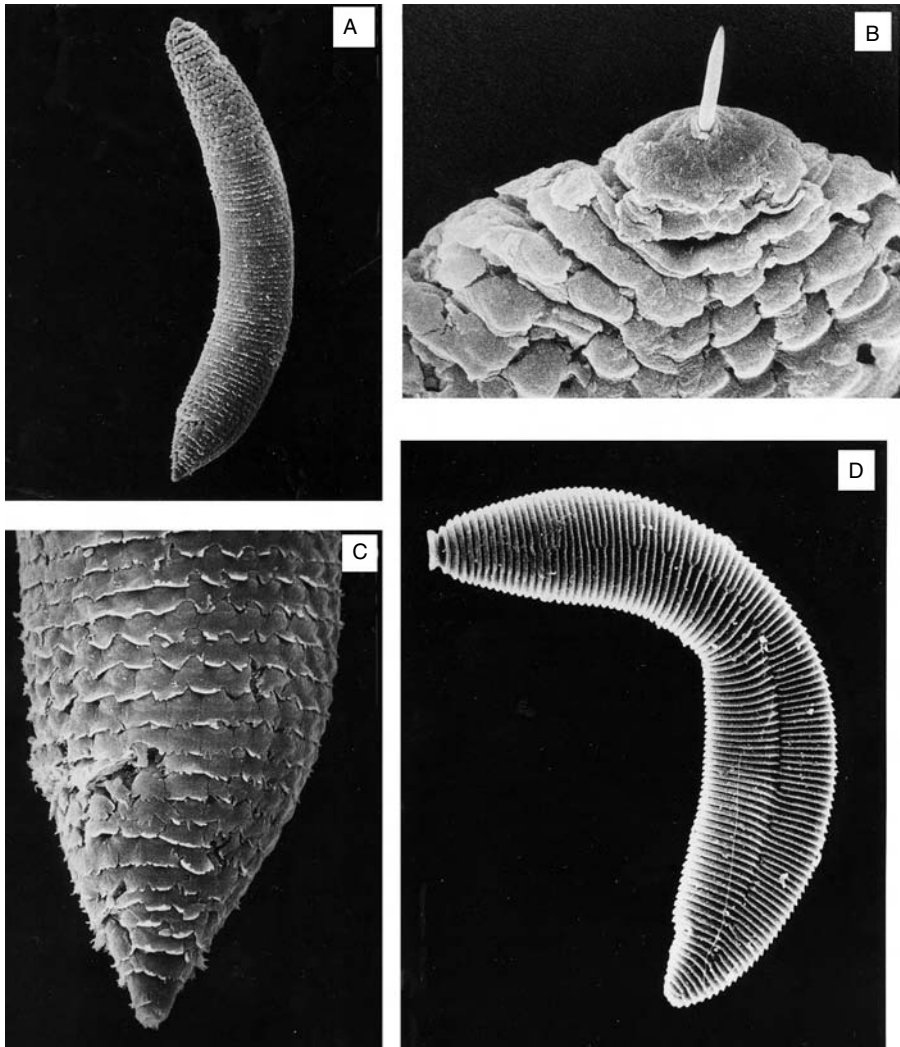
syn. *Ogma* (*Blandicephalanema* Mehta & Raski, 1971) (Siddiqi, 1986)  
 (Figs 8(a), B; 120(b), A–C)

### Diagnosis

Criconematinae. Females 0.36–0.58 mm long, with 70–88 strongly retrorse annules bearing 8–28 scales forming longitudinal rows on body; scales flap-like, each with a long spine, tipped with minute spines or one to three projections at the tip; minute spines may occur in between scales. **Cephalic region with one annule, which is rounded and dome-shaped and often reduced in size, being smaller than adjoining body annules; submedian lobes absent.** Stylet 63–98  $\mu$ m long. Vulva closed, lips conical, not modified, withdrawn from body (spine) contour, 8–15 annules from terminus. VL/VB 1.0–1.2. Tail conoid-pointed. Males with three incisures in lateral field; bursa reduced, extending to midtail; spicules 44–48  $\mu$ m long. Juveniles with eight to ten longitudinal rows of scales, each scale bearing at its tip three to five fine serrations.

### Type species

- Blandicephalanema serratum* Mehta & Raski, 1971  
 syn. *Ogma* (*Blandicephalanema*) *serratum* (Mehta & Raski, 1971) Siddiqi, 1986  
*Ogma mehrasi* Siddiqi, 1986 (was nom. nov. for *O. serratum* (Mehta & Raski, 1971) Siddiqi, 1986; (nec *Ogma serratum* (Khan & Siddiqi, 1963) Siddiqi, 1986)



**Fig. 120(b).** Scanning electron micrographs. A–C. *Blandicephalanema* sp. From New Zealand. D. *Discocriconemella limitanea* (Luc). A and D. Females. B. Female head end. C. Female tail end.

#### Other species

*Blandicephalanema bossi* Reay, 1992

*Blandicephalanema pilatum* Mehta & Raski, 1971

syn. *Ogma* (*Blandicephalanema*) *pilatum* (Mehta & Raski, 1971) Siddiqi, 1986

ETYMOLOGY. From the Greek *bland* = smooth, *kephalé* = head, and *nema* = nematode.

Species of *Blandicephalanema* are found in New Zealand and Australia. The type species occurs in grass soil in New Zealand.

**Genus *Bakernema* Wu, 1964**

(Fig. 121, A–F)

**Diagnosis**

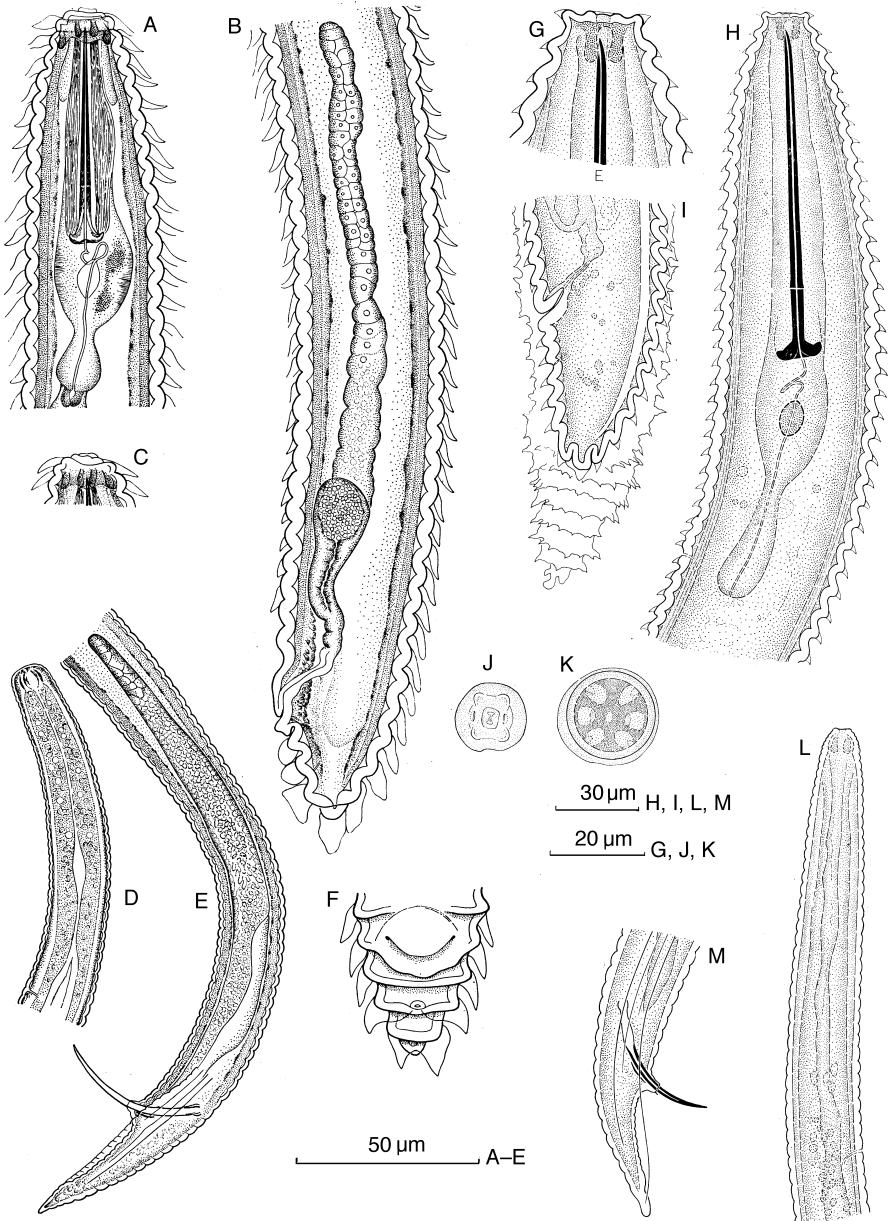
Criconematinae. Female moderately large (0.5–0.55 mm), **with transparent spine-like appendages on head and body annules** which are not easily seen in glycerine-mounted specimens. These appendages are variable in width and spacing on annules, form leaf-like flaps on tail tip, and are not arranged in definite longitudinal rows over the body. Annules 65–70 in type species, almost round. Cephalic region of two to three undifferentiated annules, not set off; labial disc elevated. Pseudolips not well developed, submedian lobes weakly developed; framework heavily sclerotized. Stylet 64–70  $\mu\text{m}$  long, in type species not flexible. Vulva on fourth to seventh annule from terminus, **anterior lip annule strongly developed, extending over it. Vagina sigmoid.** VL/VB about 1; caudal end conoid-rounded. Male cephalic region rounded, lateral field with four incisures, bursa present, low, subterminal. Spicules setose, 36–48  $\mu\text{m}$  long in type species, gubernaculum 6–7  $\mu\text{m}$  long. Hypoptygma single. Juvenile annules apparently smooth or crenate, but possibly with membranous spined outgrowths. Juveniles lack cuticular appendages in type species.

**Type species***Bakernema bakeri* (Wu, 1964) Wu, 1964**Present status***Bakernema inaequale* (Taylor, 1936) Mehta & Raski, 1971syn. *Criconema inaequale* Taylor, 1936*Criconema bakeri* Wu, 1964*Bakernema bakeri* (Wu) Wu, 1964**Other species***Bakernema dauniense* Vovlas, 1992**Remarks**

Juveniles of *Bakernema inaequale* lack the cuticular spines characteristic of the adult (Handoo & Golden, 1988). Juveniles of *B. yukonense* have crenate annules and an extra cuticular layer. *Bakernema variabile* juveniles have crenate annules near the anterior end and short, triangular outgrowths on the rest of the body. Ebsary (1981a) suggests the possibility that *Macroposthonia axeste*, *M. basili* and *M. longistyletus* may belong in *Bakernema* because of ‘extra cuticle’, as illustrated by Fassuliotis & Williamson (1959), De Grisse (1969) and De Grisse & Maas (1970), respectively. The outer layers of cuticle are also detached from the body in some species formerly assigned to *Paracriconema*. Raski & Luc (1987) transferred *Bakernema variabile* and *B. yukonense* to *Criconemella* (here assigned to *Macroposthonia*) and proposed *B. velatum* as *Criconema velatum*.

ETYMOLOGY. Prefix a patronym honouring A.D. Baker, and *nema* = nematode.

The genus is confined to North America. The type species is widely distributed in forest soils of Canada and north-eastern USA.



**Fig. 121.** A–F. *Bakernema inaequale* (Taylor) (= *Bakernema bakeri* (Wu)). G–M. *Macroposthonia variabilis* (Raski & Golden). A, C, G and H. Head ends of females. B. Posterior region of female. D and L. Anterior regions of males. E and M. Posterior regions of males. F. Posterior end of female, ventral view. I. Posterior region of female within juvenile cuticle. J. En face view. K. Cross-section through head. (A–F. After Wu (1964), courtesy *Canadian Journal of Zoology*. G–M. After Raski & Golden (1966), courtesy *Nematologica*.)

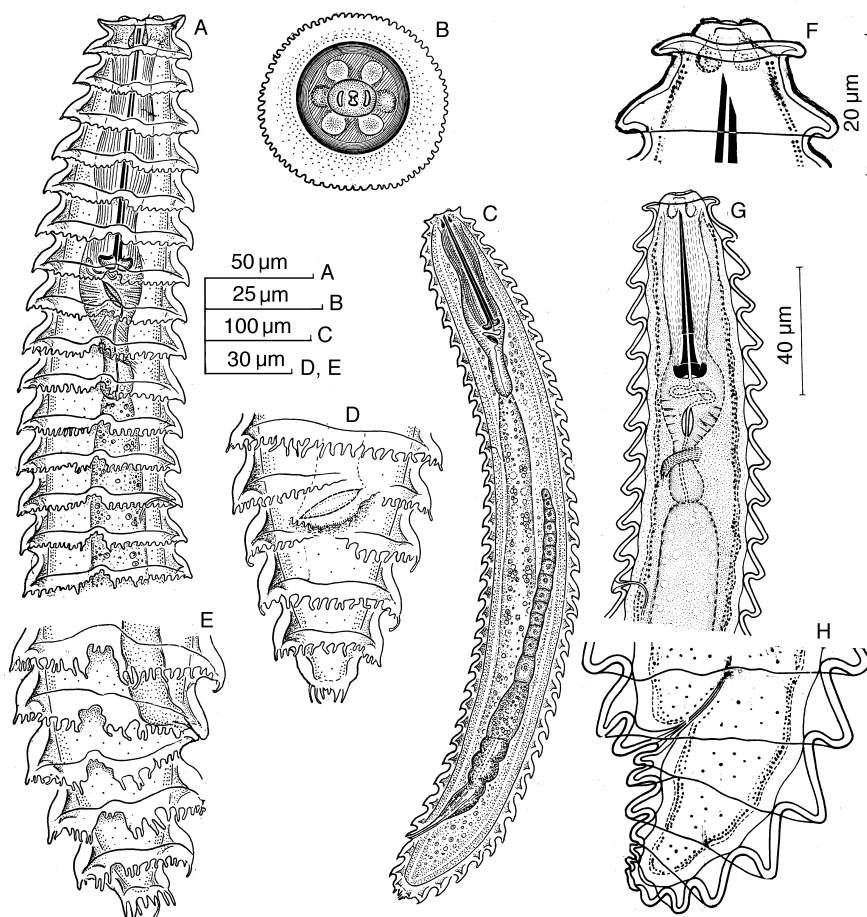
**Genus *Neolobocriconema* Mehta & Raski, 1971**syn. *Merocriconema* Raski & Pinochet, 1976*Paralobocriconema* Minagawa, 1986*Crossonemoides* Eroshenko, 1981

(Fig. 122, A–E)

**Diagnosis**

Criconematinae. Females 0.22–0.75 mm long. **Annules very coarse** (9–17  $\mu\text{m}$  wide), somewhat rounded, **36–52 in number**, crenate, finely serrated or irregularly lobed, **posteriorly lobed and/or bearing small spines**. Cephalic region **with one, rarely two, annules**, with six rather high pseudolips and **four submedian lobes**. Stylet 57–140  $\mu\text{m}$  long. Vulva closed, three to eight annules from terminus; lips conoid, anterior lip not overhanging. VL/VB 0.7–1.2. **Tail end rounded or conoid-rounded**. Juveniles with more annules than females, with eight, 12, 16 or 18 rows of spined scales. Males rare, known only in one species, with four incisures in lateral field and low bursa.

**Type species***Neolobocriconema laterale* (Khan & Siddiqi, 1964) Mehta & Raski, 1971syn. *Criconema laterale* Khan & Siddiqi, 1964*Lobocriconema laterale* (Khan & Siddiqi) De Grisse & Loof, 1965*Criconemoides lateralis* (Khan & Siddiqi) Raski & Golden, 1966*Ogma laterale* (Khan & Siddiqi) Raski & Luc, 1987*Paralobocriconema laterale* (Khan & Siddiqi) Minagawa, 1986**Other species***Neolobocriconema aberrans* (Jairajpuri & Siddiqi, 1963) Choi, 1975syn. *Criconemoides aberrans* Jairajpuri & Siddiqi, 1963*Lobocriconema aberrans* (Jairajpuri & Siddiqi) De Grisse & Loof, 1965*Criconema aberrans* (Jairajpuri & Siddiqi) Raski & Luc, 1987*Paralobocriconema aberrans* (Jairajpuri & Siddiqi) Minagawa, 1986*N. allantoideum* Eroshenko, 1980syn. *Ogma allantoideum* (Eroshenko) Raski & Luc, 1987*N. braziliense* (Raski & Pinochet, 1976) Hashim, 1984syn. *Merocriconema braziliense* Raski & Pinochet, 1976*Criconema braziliense* (Raski & Pinochet) Raski & Luc, 1985*N. calvatum* (Eroshenko, 1981) Siddiqi, 1986syn. *Crossonemoides calvatus* Eroshenko, 1981*Criconemella calvata* (Eroshenko) Raski & Luc, 1987*Mesocriconema calvatum* (Eroshenko) Loof & de Grisse, 1989*N. cataracticum* Andr  ssy, 1979syn. *Ogma cataracticum* (Andr  ssy) Raski & Luc, 1987*Paralobocriconema cataracticum* (Andr  ssy) Minagawa, 1986*N. gariepense* (Van den Berg, 1996) comb. n.syn. *Criconema gariepense* Van den Berg, 1996*N. hirakuraense* Minagawa, 1986*N. insulicum* Choi & Geraert, 1975



**Fig. 122.** A–E. *Neolobocriconema laterale* (Khan & Siddiqi). F–H. *Lobocriconema crassianulatum* (de Guiran), females. A and G. Anterior ends showing oesophagus and excretory pore. B. En face view. C. Entire body. D, E and H. Posterior ends showing vulva. F. Head end. (A–E. After Khan & Siddiqi (1964), courtesy *Nematologica*. F–H. Redrawn after de Guiran (1963).)

- syn. *Ogma* (*Homogma*) *insulicum* (Choi & Geraert) Siddiqi, 1986  
*Paralobocriconema insulicum* (Choi & Geraert) Minagawa, 1986  
*N. olearum* Hashim, 1984  
 syn. *Ogma olearum* (Hashim) Raski & Luc, 1987  
*Paralobocriconema olearum* (Hashim) Minagawa, 1986  
*N. palaniense* Muthukrishnan, 1987  
 syn. *Ogma palaniensis* (Muthukrishnan) Van den Berg, 1993  
*N. pauciannulatum* (Van den Berg, 1992) comb. n.  
 syn. *Criconema pauciannulatum* Van den Berg, 1992



*N. regularis* Rahmani, Jairajpuri & Ahmed, 1986  
syn. *Ogma regularis* (Rahmani, Jairajpuri & Ahmed) Raski & Luc, 1987

#### Remarks

*Neolobocriconema* was recognized as valid by Loof & De Grisse (1974), Khan *et al.* (1976), Andr  ssy (1979), Ebsary (1981c), Siddiqi (1986) and Rahaman & Ahmad (1996). Minagawa (1986) proposed the genus *Paralobocriconema* for *P. serratum* (Khan & Siddiqi, 1963) (type species), *P. aberrans*, *P. insulicum*, *P. cataracticum* and *P. olearum* and differentiated it from *Neolobocriconema* by moderately developed submedian lobes in the female and smooth scales in the juvenile stages. Both these characters are difficult to recognize and insufficient to distinguish *Paralobocriconema*. Raski & Luc (1987) synonymized *Paralobocriconema* with *Ogma*. *Merocriconema* Raski & Pinochet, 1976 was synonymized to *Neolobocriconema* by Hashim (1984) and to *Criconema* by Raski & Luc (1985). *Merocriconema* and *Crossonemoides* Eroshenko, 1982 are regarded here as junior synonyms of *Neolobocriconema*, which is differentiated from *Ogma* by the usual absence of scales or spines on most of the body, less than 55 body annules and usually one head annule.

ETYMOLOGY. Greek *neos* = young, new, and *Lobocriconema*.

The type species was collected from soil around roots of almond (*Prunus amygdalus* Batsch) in Srinagar, Kashmir, India. A key to *Neolobocriconema* spp. was given by Minagawa (1986).

### Genus *Lobocriconema* De Grisse & Loof, 1965

(Fig. 122, F–H)

#### Diagnosis

Criconematinae. **Annules very coarse, 8–18  $\mu\text{m}$  thick, retrorse, 24–62 in number**, smooth but finely crenate with longitudinal scratches. Cephalic annules two, differentiated. Anterior one larger than posterior, **submedian lobes present**, stylet stout, 43–106  $\mu\text{m}$  long. **Vulva open**, rarely closed, anterior lip not overhanging, three to eight annules from terminus. VL/VB 0.5–1. Tail conoid-rounded. Juveniles with 8–18 rows of smooth scales.

#### Type species

*Lobocriconema crassianulatum* (de Guiran, 1963) De Grisse & Loof, 1965  
syn. *Criconemoides crassianulatus* de Guiran, 1963  
*Nothocriconema crassianulatum* (de Guiran) Andr  ssy, 1979  
*Criconema crassianulatum* (de Guiran) Raski & Luc, 1985  
*Criconemoides deconincki* De Grisse, 1963  
*Lobocriconema deconincki* (De Grisse) Siddiqi, 1986

#### Other species

*Lobocriconema bhowaliense* Singh & Khan, 1999  
*L. brevicaudatum* (Siddiqi, 1961) De Grisse, 1967  
syn. *Criconema brevicaudatum* Siddiqi, 1961

- Mesocriconema brevicaudatum* (Siddiqi) Andrásy, 1965  
*Criconemoides brevicaudatus* (Siddiqi) Raski & Golden, 1966  
*Nothocriconema brevicaudatum* (Siddiqi) Andrásy, 1979  
*L. hlagum* (Van den Berg, 1979) Ebsary, 1981  
     syn. *Macroposthonia hлага* Van den Berg, 1979  
         *Criconemella hлага* (Van den Berg) Raski & Luc, 1981  
         *Criconema hlagum* (Van den Berg) Raski & Luc, 1985  
*L. incrassatum* (Raski & Golden, 1966) Siddiqi, 1986  
     syn. *Criconemoides incrassatus* Raski & Golden, 1966  
         *Macroposthonia incrassata* (Raski & Golden) De Grisse, 1967  
         *Nothocriconemoides incrassatus* (Raski & Golden) Loof & De Grisse, 1974  
         *Madinema incrassatum* (Raski & Golden) Khan, Chawla & Saha, 1976  
         *Criconemella incrassata* (Raski & Golden) Luc & Raski, 1981  
         *Mesocriconema incrassatum* (Raski & Golden) Loof & De Grisse, 1989  
*L. iyatomii* Minagawa, 1988  
*L. lantanium* Van den Berg, 1984  
     syn. *Criconema lantanium* (Van den Berg) Raski & Luc, 1987  
*L. lefodium* Van den Berg, 1984  
     syn. *Criconema lefodium* (Van den Berg) Raski & Luc, 1987  
*L. nasuense* Minagawa, 1988  
*L. orixae* Minagawa, 1988  
*L. pauperum* De Grisse, 1967  
     syn. *Criconemoides pauperus* (De Grisse) Luc, 1970  
         *Nothocriconema pauperum* (De Grisse) Andrásy, 1979  
         *Criconema pauperum* (De Grisse) Raski & Luc, 1985  
*L. pilosum* (Van den Berg, 1984) Loof & De Grisse, 1989  
     syn. *Criconemella pilosa* Van den Berg, 1984  
         *Macroposthonia pilosa* (Van den Berg) Siddiqi, 1986  
*L. rishikense* Singh & Khan, 1999  
*L. sabiense* Heyns, 1970  
     syn. *Nothocriconema sabiense* (Heyns, 1970) Andrásy, 1979  
         *Criconema sabiense* (Heyns) Raski & Luc, 1985  
*L. sherpai* Singh & Khan, 1999  
*L. silvum* Van den Berg, 1984  
     syn. *Criconema silvum* (Van den Berg) Raski & Luc, 1987  
*L. tessellatum* (Van den Berg, 1992) comb. n.  
     syn. *Criconema tessellatum* Van den Berg, 1992  
*L. thornei* Knobloch & Bird, 1978  
     syn. *Criconema thornei* (Knobloch & Bird) Raski & Luc, 1985

ETYMOLOGY. From Greek *lobos* = lobe (for submedian cephalic lobes), and *Criconema*.

The type species was found around roots of *Imperata cylindrica* Beauv. in Côte d'Ivoire, Africa. A key to *Lobocriconema* spp. was given by Minagawa (1988).

**Subfamily *Macroposthoniinae* Skarbilovich, 1959**  
**syn. *Macroposthoniinae* Ivanova, 1976**  
***Madinematinae* Khan, Chawla & Saha, 1976**  
***Criconemellinae* Khan & Saeed, 1985**

**Diagnosis**

*Criconematidae*. **Female:** Body arcuate or ring-like, with 42–200 retrorse annules having smooth, rough or crenate margins, but **lacking scales, spines and other cuticular appendages**. No cuticular sheath or lateral fields. Stylet and oesophagus typical of the family. **Male:** Cephalic region round, conoid or surmounted by a disc-like pad (*Discocriconemella*). Bursa low, subterminal, or absent. Spicules setose, ventrally arcuate. **Juveniles:** Body annules retrorse, smooth, with rough or crenate margins, but **lacking scales or spines**.

**Type genus**

*Macroposthonia* de Man, 1880

Other genera

*Criconemoides* Taylor, 1936

Subgenera

*Criconemoides* Taylor, 1936

*Criconemella* De Grisse & Loof, 1965

*Discocriconemella* De Grisse & Loof, 1965

*Nothocriconemoides* Maas, Loof & De Grisse, 1971

*Xenocriconemella* De Grisse & Loof, 1965

**Key to genera of *Macroposthoniinae***  
**(based on female)**

1. Vulva overhung by anterior lip ..... *Nothocriconemoides*  
    Vulva not overhung by anterior lip ..... 2
2. Vulva open; submedian lobes present, separate ..... *Macroposthonia*  
    Vulva closed; submedian pseudolips may appear as lobes, not separate ..... 3
3. Anterior cephalic annule large disc-like, distinctly offset by a collar  
    ..... *Discocriconemella*  
    Anterior cephalic annule not disc-like, not distinctly offset ..... 4
4. Anterior cephalic annule very small, surrounded by second annule; stylet  
    thin, very long and flexible ..... *Xenocriconemella*  
    Anterior cephalic annule not very small, not surrounded by second annule;  
    stylet rigid, not flexible ..... *Criconemoides*

**Relationship**

*Macroposthoniinae* differs from *Criconematinae* in lacking cuticular scales, spines or other configurations both in females and in juveniles. Females in *Hemicriconemoidinae* have smooth, round annules and a cuticular sheath, but juveniles have scales and spines like those of the *Criconematinae*. The presence of scales

and spines in juveniles of Hemicriconemoidinae and Criconematinae reflects their phylogenetic significance rather than behavioural adaptation to the environment.

### Remarks on the genera of Macroposthoniinae

De Grisse & Loof (1965) suppressed the genus *Criconemoides* and its type species, and distributed its other species among six genera: *Criconemella*, *Discocriconemella*, *Lobocriconema*, *Macroposthonia*, *Nothocriconema* and *Xenocriconemella*. Later, Loof & De Grisse (1967) re-validated and redefined *Criconemoides* and its type species (see remarks under *Criconemoides*). Luc (1970) recognized *Criconemoides* as the only valid genus in this group, and consequently proposed a large number of new combinations. Luc & Raski (1981) rejected *Criconemoides* and *Macroposthonia*, transferring their species to the genus *Criconemella*. This action was not accepted by several taxonomists but the genus *Criconemella sensu* Luc & Raski (1981) began to be used extensively by taxonomists and non-taxonomists. I strongly believe that *Criconemella sensu* Luc & Raski is a very heterogeneous group, and that *Criconemoides* and *Macroposthonia* have unjustifiably been rejected by Luc & Raski (1981). *Criconemella sensu* Luc & Raski (1981) was commented upon by Nicholas and Steward (1984) thus: 'The emended definition [of *Criconemella*] in our view is so imprecise and the number of species and synonyms so large that differential diagnosis becomes strongly uncertain. In our view such a large genus with wider and less precise limits is less useful than one with more clearly defined limits, even if some degree of overlap with other genera remains.' Castillo *et al.* (1988) agreed with Siddiqi (1986) in restricting the definition of *Criconemella* and differentiating the genus from *Macroposthonia* by the absence of four submedian lobes in the lip region, which is a derived character (= synapomorphy) for *Macroposthonia* within the Macroposthoniinae.

### The validity and universal usage of the genus *Macroposthonia*

Luc & Raski (1981) regarded *Macroposthonia* a *genus dubium* and its type species a *species dubia*. Loof & De Grisse (1989) recognized the importance of submedian lobes and other characters of *Macroposthonia* but also considered it as a *genus dubium*. They, therefore, replaced *Macroposthonia* by the next available synonym *Mesocriconema* Andr  ssy, 1965. They regarded specimens identified as *Macroposthonia annulata* as conspecific with *Mesocriconema kirjanovae*. This was also shown by De Grisse & Loof (1965).

Notwithstanding all the arguments put forward to suppress the genus *Macroposthonia*, it is possible to identify *M. annulata* as a good species. Even the original description of *M. annulata* by de Man (1880) is enough to establish it as a valid species. This description of the male of *M. annulata* and subsequent descriptions of it leave no doubt that the genus *Macroposthonia* can be differentiated from other genera in the family Criconematidae. The females found associated with similar males have been described. De Grisse & Loof (1965) collected males resembling de Man's specimens in several locations in The Netherlands, Belgium and Germany and found females associated with males at Bergen-op-Zoom, which is only about 70 km from the type locality. The females were identified as *Criconemoides kirjanovae* (now *Macroposthonia kirjanovae*). As the first revisers of the group, there is no doubt that these authors established the genus *Macroposthonia* and the species *M. annulata*. *Macroposthonia* and *M. annulata* are thus both valid.

Even if *M. annulata* and *M. kirjanovae* males as identified and described recently do not exactly agree with the description and illustrations of de Man (1880, 1884) on such minutiae as size of annules, head shape, lateral field as a plain band or with two inner incisures of the lateral field and tail tip shape, the genus still remains recognizable and thus valid. Coomans *et al.* (1990) agree that the curved acute tail with caudal alae is known only in *Macroposthonia sensu* De Grisse & Loof (1965). Nevertheless, they argued that *M. annulata* is *species dubia* on such flimsy grounds as: (i) the type is not extant; (ii) a neotype cannot be established (because the type locality, stated to be a meadow, close to the town of Leiden, The Netherlands, has been built up and so sampling for topotypes and neotypes is prevented (the ICZN allows for such sampling closest to the type locality and not exactly at the type locality); and (iii) characters of *M. annulata* prevent its identification with 'C.' *kirjanovae*, or with any other species in the group (this point is not justified because *M. annulata*, based on males, females and juveniles, was redescribed recently by Escuer *et al.*, (1991) from Lerida, Spain, and compared in detail with *M. annulata* of de Man. Scanning electron micrographs of males were provided to show that the lateral field is a single ridge, as was sketched by de Man.

Geraert & Luc (1994) gave reasons to suggest that *Macroposthonia annulata* from Spain described by Escuer *et al.* (1991) was not *M. annulata* but an undescribed species. Their comparison of males described by Escuer *et al.* with data from de Man (1880, 1884) revealed similarities in cloacal lips, absence of inner incisures in the lateral field, tail curvature and tail terminus shape posterior to lateral field, and some minor differences in anterior annulation of the body, lateral field width anterior to the cloaca, head shape and the position of the excretory pore. They concluded by stating: 'Escuer's "*annulata*" males are more similar to de Man's males than De Grisse and Loof's (1965) males but head shape, anterior annulation, details in the tail region and position of the excretory pore do not permit synonymy.' The question is not whether Escuer's species is exactly identifiable with *M. annulata* de Man 1880, *Criconemoides kirjanovae* Andr ssy, 1962 or *M. annulatiformis* De Grisse & Loof, 1967, or not, but whether these species are congeneric! The arguments put forward on their relationship clearly show that they are congeneric and hence they all belong to the same genus *Macroposthonia*. Nevertheless, great efforts by several taxonomists have thus far been made to establish that there is no species quite the same as *M. annulata* of de Man and hence the latter should not be recognized because it is based on male characters. Discussion on such small differences at species level clearly indicates that these authors are dealing with the species of the same genus. The point should be stressed again that, even if this population from Spain is not exactly identifiable with *M. annulata*, the genus is recognizable and is valid.

Escuer *et al.* (1991) had concluded: 'The classification proposed by Loof & De Grisse (1989) and Raski & Luc (1981, 1987) is not accepted here, as the reinstatement of *Macroposthonia* as a valid genus causes *Mesocriconema* Andr ssy, 1965; *Madinema* Khan, Chawla & Saha, 1976; *Seshadriella* Darekar & Khan, 1981; *Crossonemoides* Eroshenko, 1981 and *Criconemella p. parte sensu* Luc & Raski, 1981 to be regarded as junior synonyms of *Macroposthonia* de Man, 1880, agreeing with Siddiqi's (1986) classification.'

Those (including Luc & Baujard, 1998) who regard *M. annulata* as *sp. dubia*

should take into consideration the excellent description and illustration of male by de Man (1880, 1884), provided more than a hundred years ago, and compare them with the descriptions and illustrations of the males of criconematids as of today in order to appreciate the original clarity of presentation of description and illustration. Moreover, we should keep in mind that we have accepted *Tylenchus davainei* as described by Andr  ssy (1977) and not as described and sketched by Bastian (1865), who illustrated the species as having a straight and pointed female tail, a sharply conical male tail with a large bursa and flattened cap-like head, as in the genus *Ditylenchus*. Bastian's (1865) *T. davainei* may actually be *Ditylenchus dipsaci*! If this is true, then the entire Tylenchina becomes Hexatylinea, *sensu* Siddiqi (1986)! But the identity of *Tylenchus davainei* apud Andr  ssy (1977) has been accepted, so why not apply the same principle of first reviser to *M. annulata* and accept De Grisse & Loof's (1965) definition of *Macroposthonia* and of *M. annulata*? Taxonomists have accepted *Macroposthonia* and *M. annulata* throughout after De Grisse & Loof (1965) and new species have been described in the genus *Macroposthonia* by 37 taxonomists, including Bajaj, Cid del Prado, De Grisse, Ebsary, Hunt, Ivanova, Khan, Loof, Maqbool, Razjivin, Seshadri and Siddiqi (see authors in the list of *Macroposthonia* spp. below).

In 1989, Loof and De Grisse admitted, 'We also regard the identification of *Criconemoides kirjanovae* Andr  ssy, 1962 as *Macroposthonia annulata* de Man, 1880 as plausible; the two species are certainly congeneric.' These authors studied symplesiomorphic and synapomorphic characters of the Criconematidae and regarded the development of four submedian lobes on pseudolips as an apomorphy of *Macroposthonia*. They stated categorically, '*Macroposthonia* should be recognized as a separate [from *Criconemoides*–*Criconemella*] genus. The submedian lobes of *Macroposthonia* and those of *Criconemoides* cannot be considered homologous and the term should be restricted to those of the former genus. This was suggested already by Loof & De Grisse (1974).' Besides, as stated above, we should accept De Grisse & Loof (1965) as the first revisers who had established the genus *Macroposthonia* and the species *M. annulata*. *Macroposthonia* and *M. annulata* are thus both valid and widely used in literature all along.

#### Discussion on *Criconemoides*/*Criconemella*/*Xenocriconemella*

Taylor (1936) proposed the genus *Criconemoides* with *C. morgensis* (Hofm  nner) as the type species, describing ten known and four new species. The genus was differentiated from *Criconema* by the absence of scales, spines or other appendages on the body annules. Raski (1952, 1958) gave excellent descriptions and illustrations of new and known species of *Criconemoides*. Raski's (1958) and Oostenbrink's (1960) keys included 30 and 35 species of the genus, respectively.

Loof & De Grisse's (1967) definition of *Criconemoides* restricted the genus to forms with a closed vulva, four submedian cephalic lobes whose the subdorsals and subventrals of the same body side were amalgamated along the side of the labial disc, and males with bursa and four incisures in the lateral field. They recognized six valid species, considering *C. pseudohercyniensis* De Grisse & Koen, 1964 as a junior synonym of *C. morgensis* and *C. anura* (Kirjanova, 1948), *C. flandriensis* De Grisse, 1964 and *C. complexus* Jairajpuri, 1963 as synonyms of *Criconemoides informis* (Micoletzky, 1922). Ebsary (1979) added *C. pleriannulatus*.

De Grisse & Loof (1965) had suppressed the genus *Criconemoides* and its type species, and distributed its other species among six genera, since the identity of the type species was uncertain, its description was poor and the species was never found again. However, the identity of the type species and the genus was re-established by Loof & De Grisse (1967) by describing the type specimens of *C. morgensis*. The type specimens of *Criconema morgense* (two females on separate slides, one in glycerine, the other in Canada balsam, both slides labelled 'Morges Riv. 2 III 1912, *Criconema morgense*' and initialled Hofm.) were made available by Dr E. Altherr, Aigle, Switzerland in 1966–67 to D.J. Raski, P.A.A. Loof and A. De Grisse. They first found the specimens not to fit the original description of *C. morgense* (vide Luc & Raski, 1981), but Loof & De Grisse (1967), concluding that the glycerine-mounted specimen represented the true *C. morgense*, designated the specimen as neotype (actually it should be regarded as lectotype since it was one of the original specimens) and provided measurements, a good description and four excellent photographs of it (these photographs are pertaining to the neotype of *C. pseudohercyniensis*, a species considered by Loof & De Grisse (1967) as identical with *C. morgensis*). Unfortunately the neotype (= lectotype) was lost later during remounting by Loof & De Grisse (1967). Nevertheless, Loof & De Grisse's (1967) conclusion that *C. morgensis* and *C. pseudohercyniensis* are the same species should be taken seriously. Even if these two species are not synonymous with each other, they are nevertheless congeneric. Rejection of *Criconemoides* by Luc & Raski (1981) and Raski & Luc (1987) is, therefore, unjustified. Loof & De Grisse (1989) once more discussed the status of *Criconemoides morgensis* and stated, 'We are therefore of the opinion that our interpretation of 1967 was correct, and that the generic name *Criconemoides* is valid for the group of species of which *C. morgensis* (syn. *C. pseudohercyniensis*) is the type. Consequently, the valid name for the genus resulting from the synonymization of *Criconemoides* and *Criconemella*, is *Criconemoides* Taylor, 1936.' Here, *Criconemoides* is upheld as a valid genus and *Criconemella* is proposed as a subgenus of *Criconemoides*. This is done to show their inter-relatedness which is the key to their identification. The use of the subgeneric name does not affect the binomen.

*Criconemoides* (*Criconemella*) is distinctive because of its fine, often crenate annules in female, typical head shape, a closed vulva, a somewhat trapezoid postvulval body part, and the male having a tapering head, three incisures in the lateral field and a distinct bursa. *Criconemoides* (*Criconemella*) *goodeyi* fits uneasily in the subgenus since it has a conoid postvulval body part and a male with four incisures in the lateral field.

*Xenocriconemella* was synonymized to *Criconemella* by Luc & Raski (1981), who did not consider the great stylet length comparative to the body length (stylet 29–47% of the body length) sufficient to recognize the genus. Loof & de Grisse (1989) have shown that in *X. macrodorus* the second cephalic annule is very large and that it surrounds the small first annule, a character similar to that found in *Discocriconemella*, although it lacks the characteristic disc-shaped head of the latter genus. *Xenocriconemella* is supposed to be closer to *Discocriconemella* than *Criconemoides*/*Criconemella* (Loof & de Grisse, 1989) and is considered here as a valid genus.

Under Macroposthoniinae, I recognize the genera *Criconemoides* (with two

subgenera: *Criconemoides* and *Criconemella*), *Discocriconemella*, *Macroposthonia*, *Nothocriconemoides* and *Xenocriconemella*.

**Genus *Macroposthonia* de Man, 1880**

**syn. *Mesocriconema* Andr ssy, 1965**

***Madinema* Khan, Chawla & Saha, 1976**

***Seshadriella* Darekar & Khan, 1981**

***Neobakernema* Ebsary, 1981**

***Pakcriconemoides* Shahina & Maqbool, 1993**

(Figs 120, C–E; 121, G–M; 123, A–L)

**Diagnosis**

Macroposthoniinae. **Female:** Moderately large (about 0.3–0.78 mm). Annules coarse, 40–150 in number; posterior margins rounded, smooth, slightly rough, or crenate. Cephalic region with two to three annules, generally not modified or offset; pseudolips greatly reduced, laterals almost absent; **submedian lobes present, separated from each other**, first annule generally broken up into labial plates. Stylet from very small to large, rigid. **Vulva open**, directed outwards, anterior lip often lobed or spined. Tail end rounded or pointed. **Male:** Lateral field with a single ridge but with two to four incisures, rounded cephalic region, and a distinct bursa (less prominent in *M. annulata* group). **Juveniles:** Annules smooth, crenate or ornamented, but lacking scales, spines or other appendages. Male fourth-stage juveniles without stylet.

**Type species**

*Macroposthonia annulata* de Man, 1880

syn. *Criconemoides kirjanovae* Andr ssy, 1962

*Neocriconema kirjanovae* (Andr ssy) Diab & Jenkins, 1965

*Criconemella kirjanovae* (Andr ssy) Luc & Raski, 1981

*M. kirjanovae* (Andr ssy) Siddiqi, 1986

*Mesocriconema kirjanovae* (Andr ssy) Loof & De Grisse, 1989

**Other species**

*Macroposthonia alpina* Shahina & Maqbool, 1993

syn. *Macroposthonia curvata alpina* Shahina & Maqbool, 1993

*M. alticola* (Ivanova, 1976) Siddiqi, 1986

syn. *Nothocriconema alticola* Ivanova, 1976

*Mesocriconema alticola* (Ivanova) Ebsary, 1991

*M. anastomoides* (Maqbool & Shahina, 1985) Siddiqi, 1986

syn. *Criconemella anastomoides* Maqbool & Shahina, 1985

*Mesocriconema anastomoides* (Maqbool & Shahina) Loof & De Grisse, 1989

*Pakcriconemoides anastomoides* (Maqbool & Shahina) Shahina & Maqbool, 1993

*M. annulatifomis* De Grisse & Loof, 1967

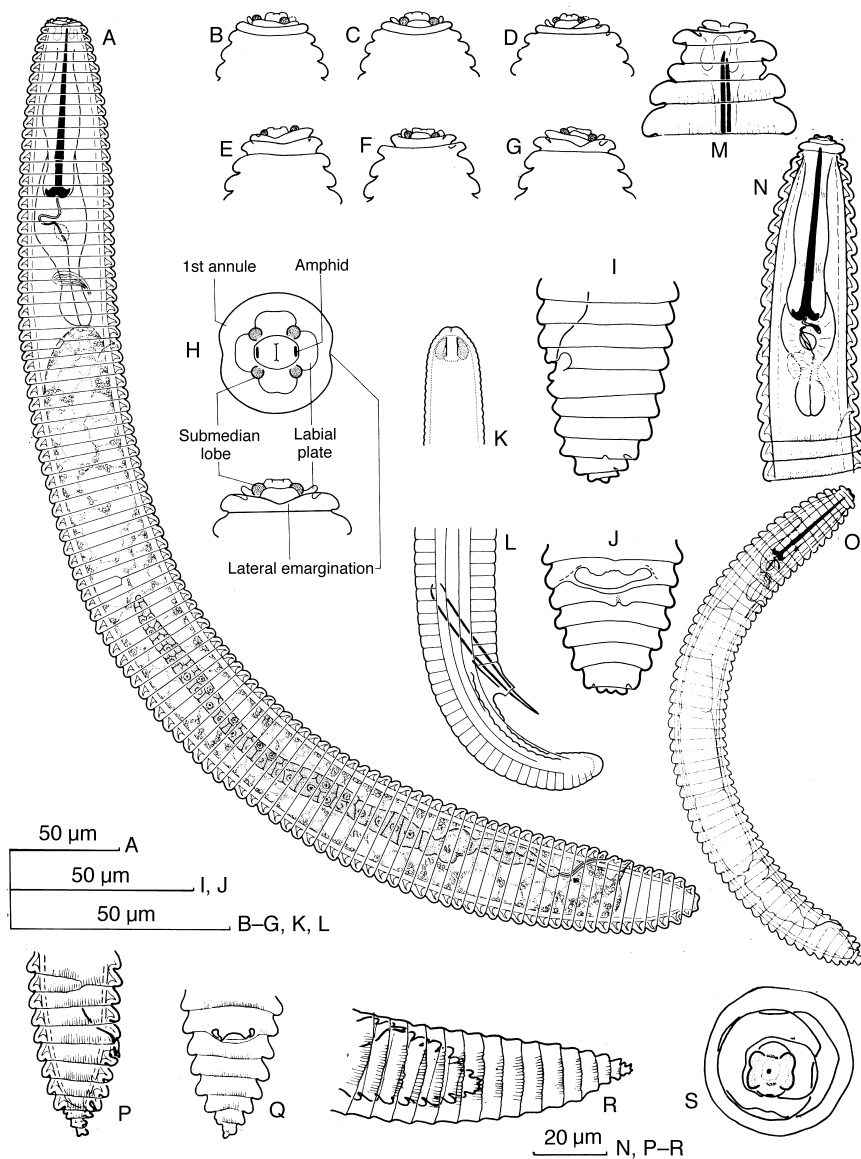
syn. *Criconemoides annulatifomis* (De Grisse & Loof) Luc, 1970

*Criconemella annulatifomis* (De Grisse & Loof) Luc & Raski, 1981

*Mesocriconema annulatiforme* (De Grisse & Loof) Loof & De Grisse, 1989

*M. antipolitana* (de Guiran, 1963) De Grisse & Loof, 1965





**Fig. 123.** A–L. *Macroposthonia xenoplax* (Raski). M–S. *Nothocriconemoides lineolatus* Maas, Loof & De Grisse. K and L. Males, remainder females. A and O. Entire body. B–H, K, M and S. Head ends. I, J, L and P–R. Tail ends. N. Oesophageal region. R. Moulting specimen. (A–L. After Orton Williams (1972): *CIH Descriptions of Plant-parasitic Nematodes*. M–S. After Maas *et al.* (1971).)

- syn. *Criconemoides antipolitanus* de Guiran, 1963  
*Criconemella antipolitana* (de Guiran) Luc & Raski, 1981  
*Mesocriconema antipolitanum* (de Guiran) Loof & De Grisse, 1989  
*Criconemoides macrolobatus* Jairajpuri & A.H. Siddiqi, 1963  
*Macroposthonia macrolobata* (Jairajpuri & A.H. Siddiqi) De Grisse & Loof, 1965
- M. axestis* (Fassuliotis & Williamson, 1959) De Grisse & Loof, 1965  
 syn. *Criconemoides axestis* Fassuliotis & Williamson, 1959  
*Criconemella axestis* (Fassuliotis & Williamson) Luc & Raski, 1981  
*Mesocriconema axeste* (Fassuliotis & Williamson) Loof & De Grisse, 1989
- M. azania* Van den Berg, 1979  
 syn. *Criconemella azania* (Van den Berg) Luc & Raski, 1981  
*Mesocriconema azania* (Van den Berg) Loof & De Grisse, 1989
- M. bakeri* (Wu, 1965) De Grisse & Loof, 1965  
 syn. *Criconemoides bakeri* Wu, 1965  
*Criconemella bakeri* (Wu) Luc & Raski, 1981  
*Mesocriconema bakeri* (Wu) Loof & De Grisse, 1989
- M. basili* (Jairajpuri, 1964) De Grisse & Loof, 1965  
 syn. *Criconemoides goodeyi* Jairajpuri, 1964, *nec* de Guiran, 1963  
*Criconemoides basili* Jairajpuri, 1964  
*Criconemella basili* (Jairajpuri) Luc & Raski, 1981  
*Nothocriconemoides basili* (Jairajpuri) Loof & De Grisse, 1974  
*Mesocriconema basili* (Jairajpuri) Loof & De Grisse, 1989  
*Macroposthonia michieli* Edward, Misra & Singh, 1968
- M. beljaevae* (Kirjanova, 1948) Ivanova, 1976  
 syn. *Criconema beljaevae* Kirjanova, 1948  
*Criconemoides beljaevae* (Kirjanova) Raski, 1958
- M. bilaspurensis* Gupta & Gupta, 1981  
 syn. *Criconemella bilaspurensis* (Gupta & Gupta) Raski & Luc, 1987  
*Mesocriconema bilaspurense* (Gupta & Gupta) Loof & De Grisse, 1989
- M. brevicauda* (Van den Berg & Spaull, 1985) comb. n.  
 syn. *Criconemella brevicauda* Van den Berg & Spaull, 1985  
*Mesocriconema brevicauda* (Van den Berg & Spaull) Loof & De Grisse, 1989
- M. brevistylus* (Singh & Khera, 1976) Ebsary, 1979  
 syn. *Criconemoides brevistylus* Singh & Khera, 1976  
*Criconemella brevistylus* (Singh & Khera) Luc & Raski, 1981  
*Mesocriconema brevistylus* (Singh & Khera) Loof & De Grisse, 1989
- M. britsiensis* Heyns, 1970  
 syn. *Criconemella britsiensis* (Heyns) Luc & Raski, 1981  
*Mesocriconema britsiense* (Heyns) Loof & De Grisse, 1989
- M. caballeroi* Cid del Prado, 1979 (nom. nud. in Cid del Prado, 1976)  
 syn. *Criconemella caballeroi* (Cid del Prado) Luc & Raski, 1981  
*Mesocriconema caballeroi* (Cid del Prado) Loof & De Grisse, 1989
- M. caelata* (Raski & Golden, 1966) De Grisse, 1967  
 syn. *Criconemoides caelatus* Raski & Golden, 1966  
*Criconemella caelata* (Raski & Golden) Luc & Raski, 1981  
*Mesocriconema caelatum* (Raski & Golden) Loof & De Grisse, 1989

- M. canadensis* Ebsary, 1981  
syn. *Criconemella canadensis* (Ebsary) Raski & Luc, 1987  
*Mesocriconema canadense* (Ebsary) Loof & De Grisse, 1989
- M. citricola* (Siddiqi, 1965) De Grisse, 1967  
syn. *Criconemoides citricola* Siddiqi, 1965  
*Criconemella citricola* (Siddiqi) Luc & Raski, 1981  
*Macroposthonia citricola* (Siddiqi) Gupta & Gupta, 1981  
*Mesocriconema citricola* (Siddiqi) Loof & De Grisse, 1989  
*Madinema maglia* Khan, Chawla & Saha, 1976  
*Criconemella maglia* (Khan *et al.*) Luc & Raski, 1981  
*Macroposthonia maglia* (Khan *et al.*) Siddiqi, 1986
- M. coomansi* De Grisse, 1967  
syn. *Mesocriconema coomansi* (De Grisse, 1967) Loof & De Grisse, 1989
- M. crassiorbus* Patil & Khan, 1983 (? syn. of *M. ornata*)  
syn. *Criconemella crassiorbus* (Patil & Khan) Raski & Luc, 1987  
*Mesocriconema crassiorbus* (Patil & Khan) Loof & De Grisse, 1989
- M. crenata* (Loof, 1964) De Grisse & Loof, 1965  
syn. *Criconemoides crenatus* Loof, 1964  
*Criconemella crenata* (Loof) Luc & Raski, 1981  
*Neocriconema crenatum* (Loof) Diab & Jenkins, 1965  
*Mesocriconema crenatum* (Loof) Andr  ssy, 1965  
*Mesocriconema crenatum* (Loof) Loof & De Grisse, 1989
- M. cufeum* Khan, Chawla & Saha, 1976  
syn. *Criconemella cufeum* (Khan *et al.*) Luc & Raski, 1981  
*Criconemella cufeum* (Khan *et al.*) Raski & Luc, 1987  
*Mesocriconema cufeum* (Khan *et al.*) Loof & De Grisse, 1989
- M. curvata* (Raski, 1952) De Grisse & Loof, 1965  
syn. *Criconemoides curvatus* Raski, 1952  
*Criconemella curvata* (Raski) Luc & Raski, 1981  
*Mesocriconema curvatum* (Raski) Loof & De Grisse, 1989  
*Criconemoides tescora* de Guiran, 1963  
*Macroposthonia tescora* (de Guiran) De Grisse & Loof, 1965  
*Mesocriconema tescorum* (de Guiran) Loof & De Grisse, 1989  
*Criconemoides nainitalensis* Edward & Misra, 1963  
*Macroposthonia nainitalensis* (Edward & Misra) De Grisse & Loof, 1965  
*Criconemoides dorsoflexus* Boonduang & Ratanaprapa, 1974  
*Macroposthonia dorsoflexa* (Boonduang & Ratanaprapa) Siddiqi, 1986  
*Macroposthonia ritteri* Doucet, 1980  
*Criconemella ritteri* (Doucet) Chavez, 1983  
*Criconemella ritteri* (Doucet) Raski & Luc, 1987  
*Mesocriconema ritteri* (Doucet) Loof & De Grisse, 1989
- M. cylindrica* (Kirjanova, 1948) Siddiqi, 1986  
syn. *Criconema cylindricum* Kirjanova, 1948  
*Criconemoides cylindricus* (Kirjanova) Raski, 1958
- M. denoudenii* De Grisse, 1967  
syn. *Criconemoides denoudenii* (De Grisse) Luc, 1970  
*Criconemella denoudenii* (De Grisse) Luc & Raski, 1981

- Mesocriconema denoudeni* (De Grisse) Loof & de Grisse, 1989
- M. dherdei* De Grisse, 1967  
syn. *Criconemoides dherdei* (De Grisse) Luc, 1970  
*Criconemella dherdei* (De Grisse) Luc & Raski, 1981  
*Mesocriconema dherdei* (De Grisse) Loof & de Grisse, 1989
- M. digiticauda* Eroshenko & Volkova, 1988  
syn. *Criconemella digiticauda* (Eroshenko & Volkova) Eroshenko & Volkova, 1997
- M. discus* (Thorne & Malek, 1968) Loof & De Grisse, 1974  
syn. *Criconemoides discus* Thorne & Malek, 1968  
*Criconemella discus* (Thorne & Malek) Luc & Raski, 1981  
*Mesocriconema discus* (Thorne & Malek) Loof & De Grisse, 1989
- M. divida* (Raski & Riffle, 1967) De Grisse, 1967  
syn. *Criconemoides divida* Raski & Riffle, 1967  
*Criconemella divida* (Raski & Riffle) Luc & Raski, 1981  
*Mesocriconema dividum* (Raski & Riffle) Loof & De Grisse, 1989
- M. douceti* Siddiqi, 1986 (was nom. nov.)  
syn. *Criconemella multiannulata* Doucet, 1982  
*M. multiannulata* (Doucet, 1982) Siddiqi, 1986 (= secondary homonym of *M. multiannulata* Eroshenko, 1980)  
*Mesocriconema multiannulatum* (Doucet) Loof & De Grisse, 1989  
*Criconemella douceti* (Siddiqi) Raski & Luc, 1987  
*Mesocriconema douceti* (Siddiqi) Ebsary, 1991
- M. ferniae* (Luc, 1959) De Grisse & Loof, 1965  
syn. *Criconemoides ferniae* Luc, 1959  
*Criconemella ferniae* (Luc) Luc & Raski, 1981  
*Mesocriconema ferniae* (Luc) Loof & De Grisse, 1989
- M. heliophila* (Ivanova & Shagalina, 1986) comb. n.  
syn. *Criconemella heliophila* Ivanova & Shagalina, 1986
- M. hispalensis* (Arias Delgado, López Pedregal & Jiménez Millán, 1963) De Grisse & Loof, 1965  
syn. *Criconemoides hispalensis* Arias Delgado, López Pedregal & Jiménez Millán, 1963
- M. hymenophora* (Wouts & Sturhan, 1999) comb. n.  
syn. *Mesocriconema hymenophorum* Wouts & Sturhan, 1999
- M. incisa* (Raski & Golden, 1966) De Grisse, 1967  
syn. *Criconemoides incisus* Raski & Golden, 1966  
*Criconemella incisa* (Raski & Golden) Luc & Raski, 1981  
*Mesocriconema incisum* (Raski & Golden) Loof & De Grisse, 1989
- M. involuta* Loof, 1987  
syn. *Mesocriconema involutum* (Loof) Loof, 1989  
*Mesocriconema involutum* (Loof) Loof & De Grisse, 1989
- M. irregularis* (De Grisse, 1964) De Grisse & Loof, 1965  
syn. *Criconemoides irregularis* De Grisse, 1964  
*Criconemella irregularis* (De Grisse) Luc & Raski, 1981  
*Mesocriconema irregulare* (De Grisse) Loof & de Grisse, 1989
- M. jessiensis* (Van den Berg, 1992) comb. n.

- syn. *Criconemella jessiensis* Van den Berg, 1992  
*Mesocriconema jessiense* (Van den Berg, 1992) Van den Berg, 1994
- M. kralli* Ivanova, 1976  
 syn. *Criconemella kralli* (Ivanova) Luc & Raski, 1981  
*Mesocriconema kralli* (Ivanova) Ebsary, 1991
- M. lamottei* (Luc, 1970) Loof & De Grisse, 1974  
 syn. *Criconemoides lamottei* Luc, 1970  
*Criconemella lamottei* (Luc) Luc & Raski, 1981  
*Mesocriconema lamottei* (Luc) Loof & De Grisse, 1989
- M. longistyletus* De Grisse & Maas, 1970  
 syn. *Madinema longistyletus* (De Grisse & Maas) Khan, Chawla & Saha, 1976  
*Nothocriconemoides longistyletus* (De Grisse & Maas) Loof & De Grisse, 1974  
*Criconemella longistyletus* (De Grisse & Maas) Luc & Raski, 1981  
*Mesocriconema longistyletus* (De Grisse & Maas) Loof & De Grisse, 1989
- M. macrodolens* (Dhanachand & Romabati, 1996) comb. n.  
 syn. *Criconemella macrodolens* Dhanachand & Romabati, 1996
- M. magnifica* Eroshenko & Tkhan, 1981  
 syn. *Criconemella magnifica* (Eroshenko & Tkhan) Raski & Luc, 1987  
*Mesocriconema magnificum* (Eroshenko & Tkhan) Loof & De Grisse, 1989
- M. magnilobata* (Darekar & Khan, 1981) Siddiqi, 1986  
 syn. *Seshadriella magnilobata* Darekar & Khan, 1981  
*Criconemella magnilobata* (Darekar & Khan) Raski & Luc, 1987  
*Mesocriconema magnilobatum* (Darekar & Khan) Loof & De Grisse, 1989
- M. malusi* Razjivin, 1974  
 syn. *Criconemella malusi* (Razjivin) Luc & Raski, 1981  
*Mesocriconema malusi* (Razjivin) Ebsary, 1991
- M. maritima* (De Grisse, 1964) De Grisse & Loof, 1965  
 syn. *Criconemoides maritimus* De Grisse, 1964  
*Criconemella maritima* (De Grisse) Luc & Raski, 1981  
*Mesocriconema maritimum* (De Grisse) Loof & De Grisse, 1989
- M. maskaka* Heyns, 1970  
 syn. *Criconemella maskaka* (Heyns) Luc & Raski, 1970  
*Mesocriconema maskaka* (Heyns) Loof & De Grisse, 1989
- M. medani* Phukan & Sanwal, 1981  
 syn. *Mesocriconema medani* (Phukan & Sanwal) Loof & De Grisse, 1989
- M. microdorus* (De Grisse, 1964) De Grisse & Loof, 1965  
 syn. *Criconema microdorus* De Grisse, 1964  
*Criconemoides microdorus* (De Grisse) De Grisse, 1964  
*Neocriconema microdorus* (De Grisse) Diab & Jenkins, 1965  
*Mesocriconema microdorus* (De Grisse) Andr  ssy, 1965  
*Criconemella microdorus* (De Grisse) Luc & Raski, 1981  
*Pakcriconemoides microdorus* (De Grisse) Shahina & Maqbool, 1993
- M. mongomorga* (Darekar & Khan, 1979) Siddiqi, 1986  
 syn. *Criconemoides mongomorgus* Darekar & Khan, 1979  
*Criconemella mongomorga* (Darekar & Khan) Luc & Raski, 1981  
*Mesocriconema mongomorgum* (Darekar & Khan) Ebsary, 1991

- M. multiannulata* Eroshenko, 1980  
 syn. *Criconemella multiannulata* (Eroshenko) Raski & Luc, 1987  
*Mesocriconema multiannulatum* (Eroshenko) Ebsary, 1991
- M. napoensis* Talavera & Hunt, 1997  
 syn. *Mesocriconema napoense* (Talavera & Hunt) Luc & Baujard, 1998
- M. neli* (Van den Berg, 1994) comb. n.  
 syn. *Mesocriconema neli* Van den Berg, 1994
- M. oachirai* Khan, Seshadri, Weischer & Mathen, 1972  
 syn. *Nothocriconema oachirai* (Khan *et al.*) Ivanova, 1976  
*Mesocriconema oachirai* (Khan *et al.*) Loof & De Grisse, 1989
- M. oblongata* Renubala, Dhanachand & Gambhir, 1991
- M. oblonglineata* (Razjivin, 1974) Siddiqi, 1986  
 syn. *Criconemoides oblonglineatus* Razjivin, 1974  
*Criconemella oblonglineata* (Razjivin) Luc & Raski, 1981  
*Mesocriconema oblonglineatum* (Razjivin) Ebsary, 1991
- M. obtusicaudata* (Heyns, 1962) Heyns, 1970  
 syn. *Criconemoides obtusicaudatus* Heyns, 1962  
*Mesocriconema obtusicaudatum* (Heyns) Loof & De Grisse, 1989
- M. onoensis* (Luc, 1959) De Grisse & Loof, 1965  
 syn. *Criconemoides onoensis* Luc, 1959  
*Criconemella onoensis* (Luc) Luc & Raski, 1981  
*Mesocriconema onoense* (Luc) Loof & De Grisse, 1989
- M. onostri* Phukan & Sanwal, 1981  
 syn. *Mesocriconema onostri* (Phukan & Sanwal) Loof & De Grisse, 1989
- M. oostenbrinki* (Loof, 1964) De Grisse & Loof, 1965  
 syn. *Criconemoides oostenbrinki* Loof, 1964  
*Neocriconema oostenbrinki* (Loof) Diab & Jenkin, 1965  
*Mesocriconema oostenbrinki* (Loof) Andr  ssy, 1965  
*Criconemella oostenbrinki* (Loof) Luc & Raski, 1981
- M. orientalis* (Rahaman & Ahmad, 1996) comb. n.  
 syn. *Mesocriconema orientale* Rahaman & Ahmad, 1996
- M. ornata* (Raski, 1958) De Grisse & Loof, 1965  
 syn. *Criconemoides cylindricus* Raski, 1952, nec. Kirjanova, 1948 (= secondary homonym)  
*Criconemoides ornatus* Raski, 1958  
*Criconemella ornata* (Raski) Luc & Raski, 1981  
*Mesocriconema ornatum* (Raski) Loof & De Grisse, 1989
- M. ornicauda* (Vovlas, Inserra & Esser, 1991) comb. n.  
 syn. *Mesocriconema ornicauda* Vovlas, Inserra & Esser, 1991
- M. oryzae* Sharma, Edward, Misra & Chandrashekar, 1992
- M. ovospermata* (Mohilal & Dhanachand, 1998) comb. n.  
 syn. *Criconemella ovospermata* Mohilal & Dhanachand, 1998
- M. palustris* (Luc, 1970) Loof & De Grisse, 1974  
 syn. *Criconemoides palustris* Luc, 1970  
*Criconemella palustris* (Luc) Luc & Raski, 1981  
*Mesocriconema palustre* (Luc) Loof & De Grisse, 1989
- M. paradenouden* (Rashid, Geraert & Sharma, 1987) comb. n.

- syn. *Criconemella paradenoudeni* Rashid, Geraert & Sharma, 1987  
*Mesocriconema paradenoudeni* (Rashid *et al.*) Loof & De Grisse, 1989
- M. paralineolata* (Rashid, Geraert & Sharma, 1987) comb. n.  
 syn. *Criconemella paralineolata* Rashid, Geraert & Sharma, 1987  
*Mesocriconema paralineolatum* (Rashid *et al.*) Ebsary, 1991
- M. paramonovi* Razjivin, 1974  
 syn. *Criconemella paramonovi* (Razjivin) Luc & Raski, 1981  
*Mesocriconema paramonovi* (Razjivin) Loof & De Grisse, 1989
- M. paranostris* Deswal & Bajaj, 1987  
 syn. *Criconemella paranostris* (Deswal & Bajaj) Raski & Luc, 1987  
*Mesocriconema paranostris* (Deswal & Bajaj) Ebsary, 1991
- M. parareedi* Ebsary, 1981  
 syn. *Criconemella parareedi* (Ebsary) Ebsary, 1982  
*Mesocriconema parareedi* (Ebsary) Loof & De Grisse, 1989
- M. paraxestis* Dhanachand & Renubala, 1991 (original spelling *paraxeste*)
- M. pelerentsi* (Sakwe & Geraert, 1991) comb. n.  
 syn. *Criconemella pelerentsi* Sakwe & Geraert, 1991
- M. peruensisformis* De Grisse, 1967  
 syn. *Criconemoides peruensisformis* (De Grisse) Luc, 1970  
*Criconemella peruensisformis* (De Grisse) Luc & Raski, 1981  
*Mesocriconema peruensisforme* (De Grisse) Loof & De Grisse, 1989
- M. peruensis* (Steiner, 1920) De Grisse & Loof, 1965  
 syn. *Hoplolaimus rusticus* var. *peruensis* Steiner, 1920  
*Iota peruensis* (Steiner) Cobb, 1924  
*Criconema rusticum* var. *peruense* (Steiner) Micoletzky, 1925  
*Criconema peruense* (Steiner) de Coninck, 1939  
*Criconemoides peruensis* (Steiner) Taylor, 1936  
*Criconemella peruensis* (Steiner) Luc & Raski, 1981  
*Mesocriconema peruense* (Steiner) Loof & De Grisse, 1989
- M. planilobata* Talavera & Hunt, 1997  
 syn. *Mesocriconema planilobatum* (Talavera & Hunt) Luc & Baujard, 1998
- M. profuses* (Wang & Wu, 1993) comb. n.  
 syn. *Criconemoides profuses* Wang & Wu, 1993
- M. pruni* (Siddiqi, 1961) De Grisse & Loof, 1965  
 syn. *Criconema pruni* Siddiqi, 1961  
*Criconemoides pruni* (Siddiqi) Raski & Golden, 1966  
*Mesocriconema pruni* (Siddiqi) Andr  ssy, 1965  
*Criconemella pruni* (Siddiqi) Luc & Raski, 1981
- M. pseudosolivaga* (De Grisse, 1964) De Grisse & Loof, 1965  
 syn. *Criconemoides pseudosolivagus* De Grisse, 1964  
*Neocriconema pseudosolivagum* (De Grisse) Diab & Jenkins, 1965  
*Mesocriconema pseudosolivagum* (De Grisse) Andr  ssy, 1965  
*Mesocriconema pseudosolivagum* (De Grisse) Loof & De Grisse, 1989  
*Criconemella pseudosolivaga* (De Grisse) Luc & Raski, 1981
- M. pulla* (Kirjanova, 1948) De Grisse & Loof, 1965  
 syn. *Criconema pullum* Kirjanova, 1948  
*Criconemoides pullus* (Kirjanova) Raski, 1958  
*Mesocriconema pullum* (Kirjanova) Ebsary, 1991

- M. punica* (Deswal & Bajaj, 1987) comb. n.  
 syn. *Criconemoides punicus* Deswal & Bajaj, 1987  
*Criconemella punica* (Deswal & Bajaj) Raski & Luc, 1987
- M. raskiensis* (De Grisse, 1964) De Grisse & Loof, 1965  
 syn. *Criconemoides raskiensis* De Grisse, 1964  
*Neocriconema raskiense* (De Grisse) Diab & Jenkins, 1965  
*Mesocriconema raskiense* (De Grisse) Andrásy, 1965  
*Mesocriconema raskiense* (De Grisse) Loof & De Grisse, 1989  
*Criconemella raskiensis* (De Grisse) Luc & Raski, 1981
- M. reedi* (Diab & Jenkins, 1966) De Grisse & Loof, 1967  
 syn. *Criconemoides reedi* Diab & Jenkins, 1966  
*Criconemella reedi* (Diab & Jenkins) Luc & Raski, 1981  
*Mesocriconema reedi* (Diab & Jenkins) Loof & De Grisse, 1989
- M. rihandi* (Edward, Misra & Singh, 1968) Loof & De Grisse, 1974  
 syn. *Criconemoides rihandi* Edward, Misra & Singh, 1968  
*Criconemella rihandi* (Edward *et al.*) Luc & Raski, 1981  
*Mesocriconema rihandi* (Edward *et al.*) Loof & De Grisse, 1989
- M. ripariensis* (Eroshenko & Volkova, 1997) comb. n.  
 syn. *Criconemella ripariensis* Eroshenko & Volkova, 1997
- M. rotundicauda* (Loof, 1964) De Grisse & Loof, 1965  
 syn. *Criconemoides rotundicauda* Loof, 1964  
*Criconemella rotundicauda* (Loof) Luc & Raski, 1981  
*Mesocriconema rotundicauda* (Loof) Loof, 1989  
*Mesocriconema rotundicauda* (Loof) Loof & De Grisse, 1989  
*Criconemoides parakouensis* Germani & Luc, 1976  
*Macroposthonia parakouensis* (Germani & Luc) Siddiqi, 1986
- M. rustica* (Micoletzky, 1915) De Grisse & Loof, 1965  
 syn. *Criconema rusticum* (Micoletzky), 1915  
*Hoplolaimus rusticus* (Micoletzky) Menzel, 1917  
*Mesocriconema rusticum* (Micoletzky) Loof & De Grisse, 1989  
*Criconema quadricorne* Kirjanova, 1948  
*Criconemoides quadricornis* (Kirjanova) Raski, 1958  
*Macroposthonia quadricornis* (Kirjanova) De Grisse & Loof, 1965  
*M. quadricornis* (Kirjanova) Ivanova, 1976  
*Mesocriconema quadricorne* (Kirjanova) Ebsary, 1991  
*Criconemoides lobatus* Raski, 1952  
*Macroposthonia lobata* (Raski) Siddiqi, 1986  
*Macroposthonia rusium* Khan, Chawla & Saha, 1976  
*Criconemella rusium* (Khan *et al.*) Luc & Raski, 1981  
*Mesocriconema rusium* (Khan *et al.*) Loof & De Grisse, 1989  
*Madinema loma* Khan, Chawla & Saha, 1976  
*Criconemella loma* (Khan *et al.*) Luc & Raski, 1981  
*Macroposthonia loma* (Khan *et al.*) Siddiqi, 1986
- M. serrata* Renubala, Dhanachand & Gambhir, 1991
- M. sicula* Vovlas, 1982  
 syn. *Criconemella sicula* (Vovlas) Raski & Luc, 1987  
*Mesocriconema sicula* (Vovlas) Loof & De Grisse, 1989



- M. sigillaria* (Eroshenko & Volkova, 1997) comb. n.  
syn. *Criconemella sigillaria* Eroshenko & Volkova, 1997
- M. similicrenata* Cid del Prado, 1979  
syn. *Criconemella similicrenata* (Cid del Prado) Luc & Raski, 1981  
*Mesocriconema similicrenatum* (Cid del Prado) Loof & De Grisse, 1989
- M. similis* (Cobb, 1918) De Grisse & Loof, 1965  
syn. *Iota similis* Cobb, 1918  
*Hoplolaimus similis* (Cobb) Micoletzky, 1922  
*Criconemoides similis* (Cobb) Chitwood, 1949  
*Mesocriconema simile* (Cobb) Ebsary, 1991
- M. solivaga* (Andrássy, 1962) De Grisse & Loof, 1965  
syn. *Criconemoides solivagus* Andrássy, 1962  
*Neocriconema solivagum* (Andrássy) Diab & Jenkins, 1965  
*Criconemella solivaga* (Andrássy) Luc & Raski, 1981  
*Mesocriconema solivagum* (Andrássy) Loof & De Grisse, 1989  
*Criconemoides rosae* Loof, 1964  
*Macroposthonia rosae* (Loof) De Grisse & Loof, 1965
- M. sosamossi* Cid del Prado, 1979 (nom. nud. in Cid del Prado, 1976)  
syn. *Criconemella sosamossi* (Cid del Prado) Luc & Raski, 1981  
*Mesocriconema sosamossi* (Cid del Prado) Loof & De Grisse, 1989
- M. sphaerocephaloides* (De Grisse, 1967) Orton Williams, 1981  
syn. *Discocriconemella sphaerocephaloides* De Grisse, 1967  
*Criconemoides sphaerocephaloides* (De Grisse) Luc, 1970  
*Madinema sphaerocephaloides* (De Grisse) Khan, Chawla & Saha, 1976  
*Criconemella sphaerocephaloides* (De Grisse) Raski & Luc, 1987  
*Mesocriconema sphaerocephaloides* (De Grisse) Loof & De Grisse, 1989
- M. sphaerocephalus* (Taylor, 1936) De Grisse & Loof, 1965  
syn. *Criconemoides sphaerocephalus* Taylor, 1936  
*Criconemella sphaerocephalus* (Taylor) Luc & Raski, 1981  
*Mesocriconema sphaerocephalus* (Taylor) Loof & De Grisse, 1989  
*Criconemoides citri* Steiner, 1949  
*Macroposthonia citri* (Steiner) Siddiqi, 1986  
*Criconemoides georgii* Prasad, Khan & Mathur, 1966  
*Macroposthonia georgii* (Prasad, Khan & Mathur) Siddiqi, 1986
- M. striatella* Eroshenko, 1980  
syn. *Criconemella striatella* (Eroshenko) Raski & Luc, 1987  
*Mesocriconema striatellum* (Eroshenko) Ebsary, 1991
- M. surinamensis* (De Grisse & Maas, 1970) Loof & De Grisse, 1971  
syn. *Discocriconemella surinamensis* De Grisse & Maas, 1970  
*Criconemella surinamensis* (De Grisse & Maas) Luc & Raski, 1981  
*Mesocriconema surinamense* (De Grisse & Maas) Loof & De Grisse, 1989  
*Discocriconemella heynsi* Van den Berg & Marais, 1995  
*Macroposthonia heynsi* (Van den Berg & Marais) comb. n.
- M. talensis* (Chaves, 1983) Siddiqi, 1986  
syn. *Criconemella talensis* Chaves, 1983  
*Mesocriconema talense* (Chaves) Loof & De Grisse, 1989
- M. tenuiannulata* (Tulaganov, 1949) Ivanova, 1976

- syn. *Criconema tenuiannulatum* Tulaganov, 1949  
    *Criconemoides tenuiannulatus* (Tulaganov) Raski & Golden, 1966  
    *Mesocriconema tenuiannulatum* (Tulaganov) Ebsary, 1991
- M. teres* (Raski, 1952) De Grisse & Loof, 1965  
    syn. *Criconemoides teres* Raski, 1952  
    *Criconemella teres* (Raski) Luc & Raski, 1981  
    *Mesocriconema teres* (Raski) Loof & De Grisse, 1989
- M. thabaum* (Van den Berg, 1996) comb. n.  
    syn. *Mesocriconema thabaum* Van den Berg, 1996
- M. tulaganovi* (Kirjanova, 1948) De Grisse & Loof, 1965  
    syn. *Criconema tulaganovi* Kirjanova, 1948  
    *Criconemoides tulaganovi* (Kirjanova) Raski, 1958  
    *Criconemella tulaganovi* (Kirjanova) Luc & Raski, 1981  
    *Mesocriconema tulaganovi* (Kirjanova) Loof & De Grisse, 1989
- M. vadensis* (Loof, 1964) De Grisse & Loof, 1965  
    syn. *Criconemoides vadensis* Loof, 1964  
    *Criconemella vadensis* (Loof) Luc & Raski, 1981  
    *Mesocriconema vadense* (Loof) Loof & De Grisse, 1989
- M. vallicola* (Ivanova, 1976) Siddiqi, 1986  
    syn. *Nothocriconema vallicola* Ivanova, 1976  
    *Mesocriconema vallicola* (Ivanova) Ebsary, 1991
- M. variabilis* (Raski & Golden, 1966) comb. n.  
    syn. *Bakernema variabile* Raski & Golden, 1966  
    *Neobakernema variabile* (Raski & Golden) Ebsary, 1981  
    *Criconemella variabilis* (Raski & Golden) Raski & Luc, 1987  
    *Mesocriconema variabile* (Raski & Golden) Loof & De Grisse, 1989
- M. wolgogica* Choi & Geraert, 1975  
    syn. *Criconemella wolgogica* (Choi & Geraert) Raski & Luc, 1987  
    *Mesocriconema wolgogicum* (Choi & Geraert) Loof & De Grisse, 1989
- M. xenoplax* (Raski, 1952) De Grisse & Loof, 1965  
    syn. *Criconemoides xenoplax* Raski, 1952  
    *Criconemella xenoplax* (Raski) Luc & Raski, 1981  
    *Mesocriconema xenoplax* (Raski) Loof & De Grisse, 1989
- M. yapoensis* (Luc, 1970) Loof & De Grisse, 1974  
    syn. *Criconemoides yapoensis* Luc, 1970  
    *Criconemella yapoensis* (Luc) Luc & Raski, 1981  
    *Mesocriconema yapoense* (Luc) Loof & De Grisse, 1989
- M. yossifovichi* (Krnjaić, 1967) Loof & De Grisse, 1974  
    syn. *Discocriconemella yossifovichi* Krnjaić, 1967  
    *Criconemella yossifovichi* (Krnjaić) Luc & Raski, 1981  
    *Mesocriconema yossifovichi* (Krnjaić) Loof & De Grisse, 1989
- M. yukonensis* (Ebsary, 1982) comb. n.  
    syn. *Bakernema yukonense* Ebsary, 1982  
    syn. *Criconemella yukonensis* (Ebsary) Raski & Luc, 1987

## Species inquirendae

- Macroposthonia anurus* (Kirjanova, 1948) Ivanova, 1976  
 syn. *Criconema anurum* Kirjanova, 1948  
*Criconemoides anurus* (Kirjanova) Raski, 1958  
*Macroposthonia kamaliei* (Khan, 1971) Siddiqi, 1986  
 syn. *Criconemoides kamaliei* Khan, 1971  
*Mesocriconema kamaliei* (Khan) Ebsary, 1991

## Nomina nuda

- Macroposthonia efficiens* Kapoor, 1983  
*M. lanatae* Kapoor, 1983  
*M. vigens* Kapoor, 1983

## Remarks

The head structure (reduction of the pseudolips, laterals being almost absent, projecting submedian lobes and, generally, first annule broken into plates), an open vulva and the four incisures of the male lateral field differentiate *Macroposthonia* from *Criconemoides*/*Criconemella*. The large number of species and the great diversity of morphological structures of *Macroposthonia* may, at times, cause difficulty in applying these differentiating criteria. Nevertheless, head and vulva shape are good and, fairly constant characters (De Grisse & Loof, 1970; Loof & De Grisse, 1974) and if carefully studied, do help in separating *Macroposthonia* species from those of *Criconemoides*/*Criconemella*.

Loof & De Grisse (1974) noted several groups in species of *Macroposthonia*. The *M. caelata* group, with small body, crenate annules and small or rudimentary submedian lobes, includes *M. caelata*, *M. divida*, *M. lamottei*, *M. microdorus*, *M. pseudosolivaga* and *M. teres* and is close to *Criconemella*. From this group two lines of development are seen:

1. The *M. annulata* group, with conoid tails, includes *M. annulata*, *M. annulatiformis*, *M. britsiensis*, *M. denoudenii*, *M. peruensisformis*, *M. peruensis* and *M. reedi*. A subgroup of this line has a prominent anterior vulva lip with two spines and a ventral contraction of the body just behind the vulva, and includes forms such as *M. axestis*, *M. dherdei* and *M. solivaga*.
2. The *M. curvata* group, with round tails, has *M. ornata* with the smallest submedian lobes, *M. curvata* and *M. xenoplax* with well-developed lobes, *M. antipolitana* and *M. vadensis* with much enlarged submedian lobes, which probably lead to the disc-like lobes found in the group comprising *M. surinamensis* and *M. yossifovichii*. The *M. curvata* group, through the *M. basili* group, leads to the genus *Nothocriconemoides*.

ETYMOLOGY. Greek *macras* = large, *posthon*, *posthonos* = penis (for spicule) but feminine in gender.

The type species was described from a male collected from moist soils in meadow and marshlands in Holland (in Leiden as reported by de Man, 1921). *Macroposthonia* spp. have a worldwide distribution.

**Genus *Criconemoides* Taylor, 1936**  
**syn. *Criconemella* De Grisse & Loof, 1965**

**Diagnosis**

Macroposthoniinae. **Female:** Small to moderately large (about 0.3–1 mm), sausage- or ring-like when relaxed. Annules crenate, rough or smooth, with round to pointed edges, 48–200 in number. Cephalic annules two to three, smaller than and not differentiated or separated by a collar from body annules. **Submedian pseudolips may be modified to appear as lobes, connected laterally** (dorsal and ventral pseudolip lobes partially fused); lateral pseudolips present but reduced. **True submedian lobes as outgrowths on submedian lobes absent.** Stylet moderately long (about 38–80 µm), usually rigid. **Vulva lips closed, conical** (anterior lip not ornamented, not overhanging), protruding to or slightly beyond body contour. Vagina straight. Tail short, conoid, convex-conoid or hemispheroidal. **Male:** Cephalic region rounded or conoid, lateral field with three to four incisures. Bursa distinct, subterminal. **Juveniles:** Annules crenate, sometime smooth, never with scales or spines. Male fourth-stage juveniles usually lacking stylet.

**Type subgenus**

*Criconemoides* Taylor, 1936

**Other subgenus**

*Criconemella* De Grisse & Loof, 1965

**Key to subgenera of *Criconemoides***

1. Body annules coarse, rounded, mostly not crenate; postvulval body region not trapezoid; male with round cephalic region and lateral field with four incisures ..... *Criconemoides*  
 Body annules fine, pointed, mostly crenate; postvulval body region somewhat trapezoid; male with conoid-rounded cephalic region and lateral field with three incisures ..... *Criconemella*

**Subgenus *Criconemoides* Taylor, 1936**

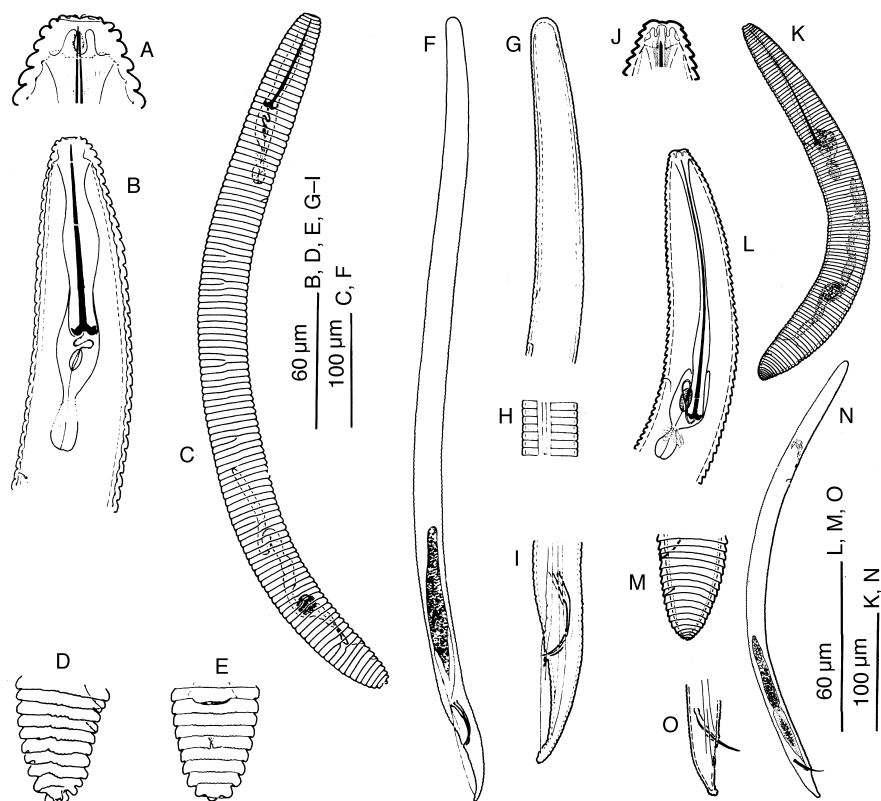
(Fig. 124, A–I)

**Diagnosis**

Genus *Criconemoides*. Body annules coarse, rounded, mostly not crenate; postvulval body region short, not trapezoid. Second cephalic annule not much wider than the first. Submedian pseudolips enlarged and may appear lobe-like and connected laterally by lateral pseudolips. Stylet rigid, moderately long. Male with round cephalic region and lateral field with four incisures.

**Type species**

*Criconemoides* (*Criconemoides*) *morgensis* (Hofmänner in Hofmänner & Menzel, 1914) Taylor, 1936  
 syn. *Criconema morgense* Hofmänner in Hofmänner & Menzel, 1914  
*Hoplolaimus morgensis* (Hofmänner) Menzel, 1917



**Fig. 124.** A–I. *Criconemoides morgensis* (Hofmänner). J–O. *Xenocriconemella microdorus* (Taylor). A–E and J–M. Females, remainder males. A and J. Head ends. B, G and L. Oesophageal regions. C, F, K and N. Entire worms. D, E M and O. Posterior ends. H. Lateral field. (A–I. After Loof (1974): CIH Descriptions of Plant-parasitic Nematodes.)

*Criconemoides pseudohercyniensis* De Grisse & Koen, 1964

*Macroposthonia pseudohercyniensis* (De Grisse & Koen) De Grisse & Loof, 1965

*Neocriconema pseudohercyniense* (De Grisse & Koen) Diab & Jenkins, 1965

*Mesocriconema pseudohercyniense* (De Grisse & Koen) Andrassy, 1965

*Macroposthonia taylori* De Grisse & Loof, 1965

*Criconemoides taylori* (De Grisse & Loof) Siddiqi, 1986

#### Other species

*Criconemoides* (*Criconemoides*) *afghanicus* Shahina & Maqbool, 1993

*C. (C.) amorphus* De Grisse, 1967 (= *Macroposthonia amorphus*, nom. nud. in De Grisse & Loof, 1965)

syn. *Criconemella amorpha* (De Grisse) Luc & Raski, 1981

*Criconemoides tafoensis* Luc, 1970

- C. (C.) *annulatus* Cobb in Taylor, 1936  
 syn. *Criconemella annulata* (Cobb in Taylor, 1936) Luc & Raski, 1981  
*Criconemoides hemisphericaudatus* Wu, 1965  
*Macroposthonia hemisphericaudata* (Wu) De Grisse & Loof, 1965  
*Criconemoides rotundicaudatus* Wu, 1965  
*Macroposthonia rotundicaudata* (Wu) De Grisse & Loof, 1965
- C. (C.) *avicenniae* (Nicolas & Stewart, 1985) Loof & De Grisse, 1989  
 syn. *Criconemella avicenniae* Nicolas & Stewart, 1985
- C. (C.) *chamoliensis* Rahaman, Ahmad & Jairajpuri, 1996
- C. (C.) *decipiens* Loof & Barooti, 1991
- C. (C.) *eroshenkoi* Siddiqi, 1986 (was nom. nov.)  
 syn. *Criconemoides mutabilis* Eroshenko, 1980  
*Criconemella eroshenkoi* (Siddiqi, 1986) Raski & Luc, 1987
- C. (C.) *featherensis* Banna & Gardner, 1993
- C. (C.) *helicus* Eroshenko & Tkhan, 1981  
 syn. *Criconemella helica* (Eroshenko & Tkhan) Raski & Luc, 1987
- C. (C.) *humilis* Raski & Riffle, 1967  
 syn. *Criconemella humilis* (Raski & Riffle) Luc & Raski, 1981
- C. (C.) *informis* (Micoletzky, 1922) Taylor, 1936  
 syn. *Hoplolaimus informis* Micoletzky, 1922  
*Criconema informe* (Micoletzky) Micoletzky, 1925  
*Macroposthonia informis* (Micoletzky) De Grisse & Loof, 1965  
*Criconemella informis* (Micoletzky) Ebsary, 1991  
*Criconemoides complexus* Jairajpuri, 1964  
*Macroposthonia complexa* (Jairajpuri) De Grisse & Loof, 1965  
*Criconemoides flandriensis* De Grisse, 1964  
*Criconemoides fimbriatus* Thorne & Malek, 1968
- C. (C.) *insignis* Siddiqi, 1961  
 syn. *Macroposthonia insignis* (Siddiqi) De Grisse & Loof, 1965  
*Criconemella insignis* (Siddiqi) Luc & Raski, 1981
- C. (C.) *inuitatus* Hoffmann, 1974  
 syn. *Criconemella inuitata* (Hoffmann) Luc & Raski, 1981
- C. (C.) *mongolensis* Andrásy, 1964  
 syn. *Criconemella mongolensis* (Andrásy) Luc & Raski, 1981
- C. (C.) *ornativulvatus* Van den Berg & Quénéhervé, 1993
- C. (C.) *pleriannulatus* Ebsary, 1979  
 syn. *Criconemella pleriannulata* (Ebsary) Luc & Raski, 1981
- C. (C.) *silvicola* Van den Berg, 1996
- C. (C.) *vernus* Raski & Golden, 1966  
 syn. *Criconemella vernus* (Raski & Golden) Luc & Raski, 1981

Species inquirendae vel dubiae et incertae sedis

- Criconemoides congolensis* (Schuurmans Stekhoven & Teunissen, 1938) Goodey, 1951  
 syn. *Criconema congolense* Schuurmans Stekhoven & Teunissen, 1938  
*Criconemella congolensis* (Schuurmans Stekhoven & Teunissen) Ebsary, 1991
- C. *heideri* (Stefanski, 1916) Taylor, 1936  
 syn. *Criconema heideri* Stefanski, 1916

- Hoplolaimus heideri* (Stefanski) Menzel, 1917  
*Criconemella heideri* (Stefanski) Ebsary, 1919  
*C. hercyniensis* Kischke, 1956 (Meyl, 1961)  
 syn. *Criconemoides morgensis hercyniensis* Kischke, 1956  
*Criconemella hercyniensis* (Kischke) Ebsary, 1991  
*C. montserrati* Arias Delgado, Jiménez Millán & López Pedregal, 1965  
 syn. *Criconemella montserrati* (Arias Delgado et al.) Ebsary, 1991  
*C. sagaensis* Yokoo, 1964  
*C. sinensis* (Rahm, 1937) T. Goodey, 1951  
 syn. *Hoplolaimus sinensis* Rahm, 1937  
*C. tenuicutis* (Kirjanova, 1948) Raski, 1958  
 syn. *Criconema tenuicute* Kirjanova, 1948  
*Macroposthonia tenuicutis* (Kirjanova) De Grisse & Loof, 1965.  
*C. xiamensis* Chongti, 1981  
 syn. *Criconemella xiamense* (Chongti), Ebsary, 1991

ETYMOLOGY. From *Criconema*, Greek *krikos* = ring, *nema* = nematode, and *oides* = shape, like.

The type species was collected on the bank of the Morges River in Switzerland.

### Subgenus *Criconemella* De Grisse & Loof, 1965

(Fig. 119, P–S; 120(a)F)

#### Diagnosis

Genus *Criconemoides*. **Female:** Body small, 0.2–0.3 mm, slender. **Annules fine, pointed**, mostly crenate, 90–200 in number. **Cephalic annules fine, two to three, smaller than and not differentiated from body annules**; six pseudolips, submedian pseudolips may appear as lobes; labial disc flat, inconspicuous. Stylet small (usually 25–41  $\mu\text{m}$ ), rigid. **Vulva lips closed**, not modified. Postvulval body part somewhat trapezoid, usually narrowing abruptly behind vulva. Male with **three incisures in lateral field**, cephalic region conoid-rounded, **bursa distinct**. Juveniles with annules crenate, but lacking scales or spines; fourth-stage juveniles without stylet.

#### Type species

- Criconemoides* (*Criconemella*) *parvus* Raski, 1952  
 syn. *Criconemoides parvus* Raski, 1952  
*Criconemella parva* (Raski, 1952) De Grisse & Loof, 1965  
*Neocriconema adamsi* Diab & Jenkins, 1965  
*Criconemoides adamsi* (Diab & Jenkins) Tarjan, 1966  
*Criconemella adamsi* (Diab & Jenkins) Siddiqi, 1986  
*Criconemoides microserratus* Raski & Golden, 1966  
*Criconemella microserrata* (Raski & Golden) Siddiqi, 1986

#### Other species

- Criconemoides* (*Criconemella*) *echinopanaxi* Mukhina, 1981  
 syn. *Criconemoides echinopanaxi* Mukhina, 1981  
*Criconemella echinopanaxi* (Mukhina) Siddiqi, 1986  
*C. (C.) goodeyi* de Guiran, 1963

- syn. *Criconemoides goodeyi* de Guiran, 1963  
*Neocriconema goodeyi* (de Guiran) Diab & Jenkins, 1965  
*Mesocriconema goodeyi* (de Guiran) Andr ssy, 1965  
*Criconemella goodeyi* (de Guiran, 1963) De Grisse & Loof, 1965  
*C. (C.) hawangiensis* (Choi & Geraert, 1995) comb. n.  
syn. *Criconemella hawangiensis* Choi & Geraert, 1995  
*C. (C.) komabaensis* (Imamura, 1931) Taylor, 1936  
syn. *Criconema komabaense* Imamura, 1931  
*Criconemella komabaensis* (Imamura) Ebsary, 1991  
*Criconemella paragoodeyi* Choi & Geraert, 1975 (syn. by Minagawa, 1995)  
*Criconemoides paragoodeyi* (Choi & Geraert) Loof & De Grisse, 1989  
*C. (C.) myungsugae* (Choi & Geraert, 1975) Loof & De Grisse, 1989  
syn. *Criconemella myungsugae* Choi & Geraert, 1975  
*C. (C.) parvulus* Siddiqi, 1961  
syn. *Criconemella parvula* (Siddiqi, 1961) De Grisse & Loof, 1965  
*C. (C.) rosmarini* (Castillo, Siddiqi & Gomez-Barcina, 1988) comb. n.  
syn. *Criconemella rosmarini* Castillo, Siddiqi & Gomez-Barcina, 1988  
*C. (C.) zavadskii* (Tulaganov, 1941) Raski, 1958  
syn. *Hoplolaimus zavadskii* Tulaganov, 1941  
*Criconemella zavadskii* (Tulaganov) De Grisse & Loof, 1965

ETYMOLOGY. From *Criconema*, and Latin suffix diminutive *-ella*.

The type species was found in soil taken around the roots of *Artemisia* sp., approx. 5 miles east of Winnemucca, Nevada, USA. A key to *Criconemella* spp. was given by Ebsary (1982).

### Genus *Xenocriconemella* De Grisse & Loof, 1965

(Fig. 124, J–O)

#### Diagnosis

Macroposthoniinae. Body small, with about 100 retrorse pointed annules. **Second cephalic annule large and surrounds the first one, which is indistinct**; cephalic annules not separated from body annules by a collar. **Stylet thin and flexible, 34–48% of body length or up to 110  $\mu$ m long**. **Vulva closed, lips forming a sleeve projecting beyond body contour**. Tail short, conoid-rounded; terminal annules small. Male with rounded head, four incisures in lateral field and a subterminal bursa. Spicules slightly arcuate, 21–22  $\mu$ m long.

#### Type species

- Xenocriconemella macrodorus* (Taylor, 1936) De Grisse & Loof, 1965  
syn. *Criconemoides macrodorus* Taylor, 1936  
*Criconemella macrodorus* (Taylor) Luc & Raski, 1981  
*Criconema goffarti* Volz, 1951  
*Criconemoides goffarti* (Volz) Goodey, 1963  
*Criconemella goffarti* (Volz) Siddiqi, 1986  
*Criconemoides juniperi* Edward & Misra, 1964  
*Criconemella juniperi* (Edward & Misra) Siddiqi, 1986



## Other species

*Xenocriconemella degrissei* Lübbers & Zell, 1989

## Note

Loof & De Grisse (1989) pointed out that the cephalic region of *Xenocriconemella macrodorus* resembles that of *Discocriconemella* in having a small anterior head annule surrounded by a large posterior one, although the head is not disc-like as in the latter genus. The vulva sleeve is prominent and is reminiscent of that in *Aulosphora*.

ETYMOLOGY. From Greek *xenos* = strange, foreign, and *Criconemella*.

The type species was found in forest near Alexandria, Virginia, USA.

**Genus *Discocriconemella* De Grisse & Loof, 1965**

syn. *Neocriconema* Diab & Jenkins, 1965

*Neocriconema* Diab, 1966

*Acrozostron* Orton Williams, 1981

(Figs 119, N & O; 120(b)D)

## Diagnosis

Macroposthoniinae. **Female:** Body 0.18–0.49 mm long, arcuate to C-shaped when relaxed. Annules 65–174, with round or angular outline and smooth, rough or crenate margins, often numerous, fine crenate and with anastomoses. **Cephalic annule appearing as a large, anteriorly flattened disc**, being wider than and separated by a collar from adjacent body annule; disc indented dorsally and ventrally or rarely circular, with submedian pseudolip areas projecting beyond its contour in some species; six pseudolips indistinct, being fused into this disc. Submedian lobes absent. Amphid apertures small pore- or slit-like or large oval. Stylet short (33–66  $\mu\text{m}$  or exceptionally long (99–113  $\mu\text{m}$ ) in *D. baforti*), rigid or flexible. **Vulva closed**, lips not modified. Postvulval body part short rounded or elongate narrow, sometimes curved dorsally. **Male:** Lateral field narrow, **with two, three or four incisures**. Cephalic region tapering, smooth, **surmounted by a distinct disc or knob of thickened cuticle**. **Bursa low, indistinct or absent**. **Juveniles:** Annules crenate, without scales or spines.

## Type species

*Discocriconemella limitanea* (Luc, 1959) De Grisse & Loof, 1965

syn. *Criconema limitaneum* Luc, 1959

*Criconemoides limitaneus* (Luc) Luc & de Guiran, 1960

*Neocriconema limitaneum* (Luc) Diab & Jenkins, 1965

*Mesocriconema limitaneum* (Luc) Andrásy, 1965

*Discocriconemella barberi* Chawla & Samathanam, 1980

*Discocriconemella repleta* Pinochet & Raski, 1976

## Other species

*Discocriconemella addisababa* Abebe & Geraert, 1995

*D. aquatica* Dhanachand & Renubala, 1991

- D. baforti* De Grisse, 1967  
 syn. *Criconemoides baforti* (De Grisse) Luc, 1970  
*Madinema baforti* (De Grisse) Khan, Chawla & Saha, 1976
- D. caudaventer* Orton Williams, 1979  
 syn. *Acrozostron caudaventer* (Orton Williams) Orton Williams, 1981
- D. colbrani* (Luc, 1970) Loof & De Grisse, 1974  
 syn. *Criconemoides colbrani* Luc, 1970
- D. conicaudata* Vovlas & Sharma, 1989
- D. degrissei* Loof & Sharma, 1980
- D. dimorphicauda* Vovlas, Ferraz & dos Santos, 1989
- D. discolabia* (Diab & Jenkins, 1966) De Grisse, 1967  
 syn. *Criconemoides discolabia* Diab & Jenkins, 1966
- D. elettariae* Sharma & Edward, 1985
- D. glabrannulata* De Grisse, 1967  
 syn. *Criconemoides glabrannulatus* (De Grisse) Luc, 1970  
*Madinema glabrannulatum* (De Grisse) Khan, Chawla & Saha, 1976
- D. gufraensis* Van den Berg & Quénéhervé, 1997
- D. hensungica* Choi & Geraert, 1975  
 syn. *Acrozostron hensungicum* (Choi & Geraert) Orton Williams, 1981
- D. inarata* Hoffmann, 1974
- D. macramphidia* De Grisse, 1967  
 syn. *Criconemoides macramphidia* (De Grisse) Luc, 1970  
*Madinema macramphidia* (De Grisse) Khan, Chawla & Saha, 1976  
*Acrozostron macramphidia* (De Grisse) Orton Williams, 1981
- D. mauritiensis* (Williams, 1960) De Grisse & Loof, 1965  
 syn. *Criconemoides mauritiensis* Williams, 1960
- D. mineira* Vovlas, Ferraz & dos Santos, 1989
- D. morelensis* Cid del Prado Vera & Loof, 1985
- D. oryzae* Rahman, 1987
- D. pannosa* Sauer & Winoto, 1975  
 syn. *Acrozostron pannosum* (Sauer & Winoto) Orton Williams, 1981
- D. paraglabrannulata* Vovlas & Sharma, 1989
- D. perseae* Cid del Prado Vera & Loof, 1985
- D. recens* Khan, Seshadri, Weischer & Mathen, 1971  
 syn. *Madinema recens* (Khan *et al.*) Khan, Chawla & Saha, 1976
- D. retroversa* Sauer & Winoto, 1975  
 syn. *Acrozostron retroversum* (Sauer & Winoto) Orton Williams, 1981
- D. serrata* Dhanachand & Romabati, 1996
- D. spermata* Mohilal & Dhanachand, 1998
- D. theobromae* (Chawla & Samathanam, 1980) Raski & Luc, 1987  
 syn. *Madinema theobromae* Chawla & Samathanam, 1980 (original spelling *theobromi*)  
*Macroposthonia theobromae* (Chawla & Samathanam, 1980) Siddiqi, 1986  
*Mesocriconema theobromae* (Chawla & Samathanam) Ebsary, 1991
- D. uruguayensis* Vovlas & Lamberti, 1997

## Note

*Acrozostron* Orton Williams, 1981 was proposed by splitting the genus *Discocriconemella* into two groups, with *A. caudaventer* (= *Discocriconemella caudaventer*) as the type species, mainly on the character of the shape of the cephalic disc and large, open amphidial apertures. However, species in the two genera still show considerable variation in distinguishing characters and hence *Acrozostron* is not recognized here. *Discocriconemella heynsi* Van den Berg & Marais, 1995 is here transferred to *Macroposthonia*.

ETYMOLOGY. Greek *diskos* = disc (for cephalic annule), and *Criconemella*.

The type species was collected around roots of *Cinchona succirubra* Pav., at Seredou, Guinea, Africa. A key to *Discocriconemella* spp. was given by Ebsary (1982).

### Genus *Nothocriconemoides* Maas, Loof & De Grisse, 1971

(Fig. 123, M–S)

#### Diagnosis

Macroposthoniinae. **Female:** Total body annules in type species 57–64; annules with fine longitudinal striae making margins look finely crenate, lacking anastomoses. Cephalic region offset by basal annule being smaller and round; anterior annule collar-like, retrorse, much larger than the basal annule. **Lip area with four prominent submedian lobes.** Stylet 68–80  $\mu\text{m}$  long in type species. **Vulva closed, anterior bilobed lip projecting backwards. Vagina sigmoid.** Tail conoid to an acute or subacute terminus. **Juveniles:** With crenate annules, without rows of scales or spines; cephalic annules not offset collar-like.

#### Type species

*Nothocriconemoides lineolatus* Maas, Loof & De Grisse, 1971

#### Other species

*Nothocriconemoides crenulatus* Ivanova, 1984

ETYMOLOGY. Greek *nothos* = false, and *Criconemoides*.

The type species was found in sandy soil in a forest near Carolina in Surinam.

### Subfamily Hemicriconemoidinae Andr ssy, 1979

#### Diagnosis

Criconematidae. **Female:** Body enclosed in a cuticular sheath, attached to it at head, vulva and sometimes tail tip. Annules on body and sheath equal in number, **round** or occasionally retrorse, lacking scales, spines or other appendages; sheath annules often flattened, sometimes with scratches, but lacking lateral fields. Stylet and oesophagus typical of the family. Tail end conoid or rounded. **Male:** Body sheath absent. Lateral field usually with four incisures. Cephalic region rounded or conoid-rounded. Bursa low, subterminal, almost terminal, or absent. Spicules slender,

ventrally arcuate. **Juveniles:** No body sheath. **Annules with scales** which are smooth, dentate or spined and arranged usually in alternating rows or irregularly.

#### Type genus

*Hemicriconemoides* Chitwood & Birchfield, 1957

No other genus.

#### Genus *Hemicriconemoides* Chitwood & Birchfield, 1957

**syn. *Iota* Cobb, 1913, nec *Iota* Saussure, 1855 (= Hymenoptera)**

(Fig. 125, A–M)

#### Diagnosis

Hemicriconemoidinae. Female elongate-cylindrical, **with double cuticle**; outer one sheath-like, attached to body at head, vulva and sometimes at tail tip; annules of sheath and body round and flat, or rarely retrorse (*H. minor*); lacking scales, spines or other appendages; 50–158 in number, with or without lateral grooves. Female cephalic region with two, rarely three annules, continuous or offset, variable in shape. Pseudolips inconspicuous, **submedian lobes absent, rarely present (*H. coronatus*)**. Stylet elongate, with **anteriorly cupped knobs appearing anchor-shaped** (rarely spheroidal). Vulva open or closed, with or without lateral cuticular flaps. Female tail variable, bluntly rounded to pointed. Males usually with four incisures in lateral field, cephalic region rounded or conoid-rounded, tail conoid to subcylindroid and bursa, when present, low subterminal or terminal (absent in type species). Spicules setose, arcuate. Gubernaculum simple, small. Juveniles with single cuticle, with smooth, dentate or spined scales, arranged in longitudinal, usually alternating rows, or irregularly on body, rarely without scales or spines (*H. minor*, *H. coronatus*); stylet knobs anchor-shaped.

#### Type species

*Hemicriconemoides wessoni* Chitwood & Birchfield, 1957

syn. *Hemicycliophora wessoni* (Chitwood & Birchfield) Goodey, 1963

*Hemicriconemoides annulatus* Pinochet & Raski, 1975

#### Other species

*Hemicriconemoides affinis* Germani & Luc, 1970

*H. alexis* Vovlas, 1980

*H. amurensis* Eroshenko & Volkova, 1986

*H. brachyurus* (Loos, 1949) Chitwood & Birchfield, 1957

syn. *Criconemoides brachyurus* Loos, 1949

*Hemicycliophora brachyurus* (Loos) Goodey, 1963

*Hemicriconemoides sacchariae* Heyns, 1970

*Hemicriconemoides intermedius* Dasgupta, Raski & Van Gundy, 1969

*Hemicriconemoides promissus* Vovlas, 1980

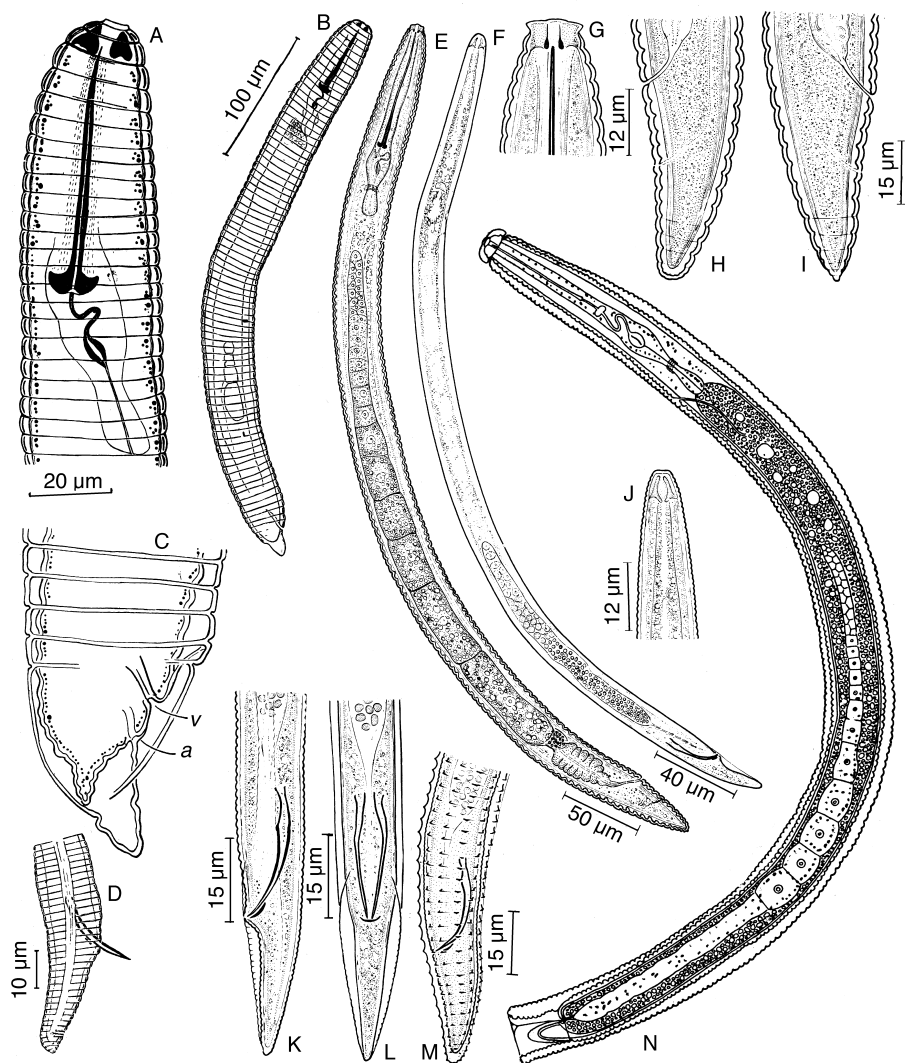
*H. brevicaudatus* Dasgupta, Raski & Van Gundy, 1969

*H. californianus* Pinochet & Raski, 1975

*H. camelliae* Zhang, 1998

*H. capensis* Van den Berg, 1990

*H. cedrusmontanus* Van den Berg & Meyer, 1991



**Fig. 125.** A–D. *Hemicriconemoides wessoni* Chitwood & Birchfield. E–M. *Hemicriconemoides mangiferae* Siddiqi. N. *Colbraniium truncatum* (Colbran). A. Oesophageal region of female. B, E and N. Females. C, H and I. Postvulval regions. a, anus; v, vulva. D, K and L. Tail ends of males. F. Male. G. Head end of female. J. Head end of male. M. Tail end of moulting male juvenile. (A–D. After Chitwood & Birchfield (1957). E–M. After Siddiqi (1961a), courtesy Helminthological Society of Washington. N. After Colbran (1956).)

- H. chitwoodi* Esser, 1960  
syn. *Hemicycliophora chitwoodi* (Esser) Goodey, 1963
- H. cocophillus* (Loos, 1949) Chitwood & Birchfield, 1957  
syn. *Criconemoides cocophillus* Loos, 1949  
*Hemicycliophora cocophilla* (Loos) Goodey, 1963
- H. communis* Edward & Misra, 1964  
syn. *Criconema mangiferum* Edward & Misra, 1963  
*Hemicriconemoides mangiferus* (Edward & Misra) Siddiqi, 1986
- H. conicaudatus* Phukan & Sanwal, 1983
- H. coronatus* Reay & Colbran, 1986
- H. digitatus* Reay & Colbran, 1986
- H. fujianensis* Zhang, 1998
- H. gabrici* (Yeates, 1973) Raski, 1975  
syn. *Paratylenchus gabrici* Yeates, 1973
- H. gaddi* (Loos, 1949) Chitwood & Birchfield, 1957  
syn. *Criconemoides gaddi* Loos, 1949  
*Hemicycliophora gaddi* (Loos) Goodey, 1963
- H. ghaffari* Maqbool, 1982
- H. insignis* Dasgupta, Raski & Van Gundy, 1969
- H. kanayaensis* Nakasono & Ichinohe, 1961  
syn. *Hemicriconemoides ureshinoensis* Yokoo, 1963
- H. longistylus* Rahman, 1987
- H. mangiferae* Siddiqi, 1961 (syn. of *H. strictathecatus* for Decraemer & Geraert, 1996)  
syn. *Hemicriconemoides litchi* Edward & Misra, 1964  
*Hemicriconemoides birchfieldi* Edward, Misra & Singh, 1965  
*Hemicriconemoides aberrans* Phukan & Sanwal, 1983
- H. mehdii* Suryawanshi, 1971
- H. microdoratus* Dasgupta, Raski & Van Gundy, 1969 (syn. of *H. cocophillus* for Germani & Luc, 1970)
- H. minor* Brzeski & Reay, 1982
- H. minutus* Esser, 1960  
syn. *Hemicycliophora minuta* (Esser) Goodey, 1963
- H. neobrachyurus* Dhanachand & Jairajpuri, 1980
- H. nitidus* Pinochet & Raski, 1975
- H. ortonwilliamsi* Ye & Siddiqi, 1994
- H. parataiwanensis* Decraemer & Geraert, 1992
- H. parvus* Dasgupta, Raski & Van Gundy, 1969
- H. pseudobrachyurus* De Grisse, 1964
- H. rotundus* Ye & Siddiqi, 1994
- H. scottolamassesei* Germani & Anderson, 1991
- H. silvaticus* Eroshenko & Volkova, 1985
- H. sinensis* Vovlas, 1988
- H. snoecki* Doorsselaere & Samsoen, 1982
- H. strictathecatus* Esser, 1960  
syn. *Hemicycliophora strictathecata* (Esser) Goodey, 1963
- H. sunderbanensis* Ganguly & Khan, 1982

*H. taiwanensis* Pinochet & Raski, 1975  
*H. variabilis* Rahaman & Ahmad, 1995  
*H. varionodus* Choi & Geraert, 1972

### Species inquirenda

*Hemicriconemoides squamosus* (Cobb, 1913) Siddiqi & Goodey, 1964  
 syn. *Iota squamosa* Cobb, 1913  
*Hoplolaimus squamosus* (Cobb) Menzel, 1917  
*Criconema squamosum* (Cobb) Taylor, 1936  
*Ogma squamosum* (Cobb) Schuurmans Stekhoven & Teunissen, 1938

### Remarks

The genus *Hemicriconemoides* was proposed by Chitwood & Birchfield (1957) as an intermediate genus between *Criconemoides* and *Hemicycliophora*; *H. wessoni* was made the type species. To this genus Chitwood & Birchfield (1957) assigned *H. biformis* and *H. floridensis* (now in *Hemicycliophora*) and three species described by Loos (1949) as *Criconemoides*. In his book, Goodey (1963) synonymized *Hemicriconemoides* with *Hemicycliophora*, but Siddiqi & Goodey (1964) reinstated the former as a valid genus, mainly on the basis of the anchor-shaped stylet base and scaled juveniles. They resurrected *Iota squamosa* Cobb, 1913 and proposed the synonymies of *H. mangiferae* and *H. strictathecatus* with it. However, since *Iota squamosa* was based on juvenile specimens and there was considerable difference in the length of the juveniles, these synonymies have not been upheld by subsequent workers, and the presence of rounded knobs in *H. strictathecatus* has been the basis for recognizing this species as different from *H. mangiferae*. Decraemer & Geraert (1996) synonymized *H. mangiferae*, *H. litchi*, *H. birchfieldi* and *H. aberrans* with *H. strictathecatus*. I studied type specimens of *H. strictathecatus* and specimens of this species from Fiji Islands collected by the late Mr Orton Williams and found that it had more compact and rounded stylet knobs, a consistently longer stylet and a larger number of longitudinal rows of scales in juveniles than *H. mangiferae* and hence the two species are distinct. Dasgupta *et al.* (1969) revised the genus and gave a detailed account of five new species and other valid species. *Hemicriconemoides* spp. show five types of lip pattern (Decraemer & Geraert, 1992a) and thus the group appears to be heterogeneous.

ETYMOLOGY. From prefix of *Hemicycliophora*, Greek *hemi* = half, and *Criconemoides* (for sharing characters of *Hemicycliophora* and *Criconemoides*).

The type species was found on roots of *Myrica cerifera* L. in Alturas, Florida, USA. *Hemicriconemoides* spp. are widely distributed in warmer areas, particularly in south and southeast Asia, Africa and southern USA. They attack several agricultural crops and fruit trees, such as maize, black pepper, tea, litchi, mango, banana, date and pineapple. A key to species is given by Esser and Vovlas (1990).

## SUPERFAMILY HEMICYCLIOPHOROIDEA SKARBILOVICH, 1959 (SIDDIQI, 1980)

### Diagnosis

Criconematina. **Body moderate to large (0.6–2.0 mm), vermiform, straight to arcuate upon relaxation, with thick cuticle and coarse round annules numbering over 200.** Juveniles and females have extra cuticle as a protective sheath, except in *Caloosia*. Lateral fields present except in females of *Caloosia* and of a few other genera. Female cephalic region with one to three annules, with a labial disc but **lacking submedian lobes.** **Stylet in juveniles and females elongated** (over 50  $\mu\text{m}$  long in females), **basal knobs rounded**, usually posteriorly sloping. Oesophagus criconematoid, with a **short broad isthmus amalgamated with basal bulb.** Intestine syncytial, vacuolated, usually extending anteriorly over basal bulb, subterminal; lips variously modified. Monodelphic, prodelphic. Female tail usually elongate-conoid to filiform but may be cylindroid or rarely hemispherical. Males with degenerated oesophagus, no stylet, an elongated tail and **prominent bursa** that rarely covers more than half of the tail. **Spicules setaceous, long, usually strongly curved to become semicircular, U- or hook-shaped** (Hemicycliophoridae), but may be arcuate (*Loofia*) or straight (Caloosiidae). Gubernaculum fixed. Cloacal lips usually elongated to form a penial tube. Hypoptygma single, seta-like, at posterior lip of cloaca.

### Type family

Hemicycliophoridae Skarbilovich, 1959

### Other family

Caloosiidae Siddiqi, 1980

### Key to families of Hemicycliophoroidea

1. Females and juveniles with or without a membranous body sheath; cephalic annules separated; vulva flush with body contour, overhung by its anterior lip; spicules straight ..... **Caloosiidae**
- Female and juveniles with a thick body sheath; cephalic annules not separated; vulva rarely flush with body contour but then not overhung by its anterior lip; spicules arcuate, semicircular, U- or hook-shaped ..... **Hemicycliophoridae**

## FAMILY HEMICYCLIOPHORIDAE (The sheath nematodes)

The presence of a body sheath as a second cuticle is the most important feature of these nematodes. The sheathed juveniles are not found in any other tylenchid group. Johnson *et al.* (1970) pointed out that a seven-layered sheath in females and juveniles and a four-layered sheath in males of *Hemicycliophora* have no parallel in the Nematoda. The body cuticle and the sheath cuticle are produced simultaneously at each moult and hence the two are an integral part of the cuticle. After the final moult, the cuticle (body cuticle + sheath cuticle) of the female *H. arenaria* is the fifth cuticle but that of the male is the sixth cuticle (Johnson *et al.*, 1970). The



juveniles have a well-developed stylet and feed, but the male juveniles lose their stylet at the final moult. The male tail of *Hemicycliophora* spp. is larger than that of the female. This led Loof (1976) to believe that the male tail of *H. typica* was the postgenital part of the body and that a cloaca and male anus were absent in that species. Siddiqi (1980b) reported that in *H. penetrans* a cloaca is formed as in other nematodes, and that the elongation of the male tail occurs soon after the male emerges from the final juvenile cuticle.

*Hemicycliophora parvana* is pathogenic to celery in Florida, USA (Tarjan, 1952). *Hemicycliophora arenaria* parasitizes rough lemon, tomato and other cultivated and non-cultivated plants in California, USA. Its life cycle is completed in 15–18 days; 30–32°C is the optimum temperature for the development. The juveniles feed on tomato seedlings by thrusting their stylet two to three cells deep into the root. The saliva is injected into the root cell during a quiescent period of 1–2 h. Meanwhile, an adhesive plug is formed around the stylet, which seals the nematode head to the root. Then the median bulb pulsates and food is drawn in, the feeding lasting for 2–6 days until the food cell becomes empty. Feeding at the root tips causes galls as the cells in the meristem divide rapidly. It was also found that, in infested field plots, tomato and squash yields were 10–20% less than in non-infested plots (McElroy & Van Gundy, 1968). *Aulosphora indica*, *A. osmani* and *A. penetrans* are found in India on cultivated and non-cultivated plants. *Loofia* spp. occur mostly in Europe and North America. Loof (1968) recorded *L. thienemanni* widely distributed in The Netherlands, occurring in orchard soils, in scrub nurseries, in agricultural land and on ditch banks, the species being moisture-loving.

In 1921, de Man described a male nematode having an obscure oesophagus, no stylet and large semicircular spicules, and named it *Hemicycliophora typica*. Later, in 1925, Micoletzky described a female nematode having a well-developed oesophagus and stylet as *Procriconema membranifer*, and transferred *Tylencholaimus aquaticus* Micoletzky and *Hoplolaimus thienemanni* Schneider to *Procriconema*. *Procriconema* was assigned to the Criconematinae by Taylor (1936) in his revision of this subfamily, but *Hemicycliophora* remained an obscure genus until 1948, when Loos in Ceylon found both males and females together, which agreed with the descriptions of the two nematodes. Loos (1948) consequently synonymized *Procriconema* with *Hemicycliophora* and transferred its species to the latter. He also described a new species, *H. longicaudata*.

Tarjan (1952) and Thorne (1955) reviewed the genus *Hemicycliophora* and gave differential keys to seven and 22 species, respectively. Thorne (1955) described 15 new species and prophesied a new genus for *H. longicaudata* Loos. The new genus was erected by Siddiqi & Goodey (1964), who named it *Caloosia* after C.A. Loos. They reviewed the taxonomy of the family Criconematidae and reinstated *Hemicriconemoides* Chitwood & Birchfield, previously synonymized to *Hemicycliophora* by Goodey (1963). Loof (1968) reviewed the taxonomy of *Hemicycliophora* and the status of its type species and described 12 species, five of which were new, mostly from Europe.

Skarbilovich (1959) proposed the subfamily Hemicycliophorinae, which was raised to family and superfamily by Geraert (1966) and Siddiqi (1980b), respectively.

Brzeski (1974) and Eroshenko (1976) produced major reviews on the species of *Hemicycliophora* and *Caloosia*, providing descriptions and differential keys. Brzeski

(1974) for the first time assigned *Hemicriconemoides* to the subfamily Hemicycliophorinae, but Andr  ssy (1979) proposed a separate subfamily for it. Andr  ssy also proposed the genus *Colbranium* to accommodate *Hemicycliophora truncata* Colbran. Siddiqi (1980b) erected two more genera for some of the existing species of *Hemicycliophora*, namely *Aulosphora* and *Loofia*, and proposed the family Caloosiidae. He also proposed a new suborder, Criconematina, and assigned Hemicycliophoroidea to it.

## Family Hemicycliophoridae Skarbilovich, 1959 (Geraert, 1966)

### Diagnosis

Hemicycliophoroidea. **Females and juveniles with body sheath as thick as body cuticle**, usually with lateral fields. Cephalic annules not modified or separated. Vulva over half body width long, usually marked by recessed body contour behind it; lips modified and projecting (except in *Loofia*). Vagina straight, curved, not sigmoid. Males with smooth, offset cephalic region, framework in lateral view appearing as 'spectacle mark' and tail longer than that of female. Spicules arcuate (*Loofia*), semi-circular (*Hemicycliophora*) or U- and hook-shaped (*Aulosphora*). Cloacal lips elongated to form a penial tube, anterior to which body usually deeply recessed. Bursa covering less than one-third of tail (except in *Colbranium*).

### Type subfamily

Hemicycliophorinae Skarbilovich, 1959

No other subfamily.

## Subfamily Hemicycliophorinae Skarbilovich, 1959

### Diagnosis

Hemicycliophoridae, with characters of the family.

### Type genus

*Hemicycliophora* de Man, 1921

### Other genera

*Aulosphora* Siddiqi, 1980

*Colbranium* Andr  ssy, 1979

*Loofia* Siddiqi, 1980

### Key to genera of Hemicycliophorinae

1. Female cephalic region set off by deep constriction; vulva subterminal; bursa covering most of tail ..... *Colbranium*  
     Female cephalic region not set off by a deep constriction; vulva not subterminal; bursa covering less than one-third of tail ..... 2
2. Vulva lips round, not modified; spicules arcuate ..... *Loofia*  
     Vulva lips modified, projecting; spicules strongly curved ..... 3

3. Vulva lips usually divergent, less than three body annules long; spicules semicircular; pre- and postanal stretches of bursa almost equal ..... *Hemicycliophora*  
 Vulva lips tubular, three or more body annules long; spicules U- or hook-shaped; preanal stretch of bursa three to four times that of postanal ..... *Aulosphora*

### Genus *Hemicycliophora* de Man, 1921

syn. *Procriconema* Micoletzky, 1925

(Figs 15, C & D; 126, A–D)

#### Diagnosis

Hemicycliophorinae. Cephalic region broadly rounded, continuous with body. **Body conspicuously recessed just behind vulva and anterior to base of penial tube.** Female and juvenile tails elongate-conoid, filiform or cylindroid, rarely hemispherical. Vulva lips modified, pointed, divergent, less than three body annules long. **Spicules semicircular.** Cloacal lips elongated to form a penial tube, which is less than one body width long and directed outward and forward. **Pre- and postanal stretches of bursa almost equal.**

#### Type species

*Hemicycliophora typica* de Man, 1921

syn. *Procriconema membranifer* Micoletzky, 1925

*Hemicycliophora membranifer* (Micoletzky) Loos, 1948

#### Other species

*Hemicycliophora aberrans* Thorne, 1955

*H. adolia* Khurramov, 1985

*H. amchitkaensis* Bernard, 1982

*H. andrassyi* Brzeski, 1974

*H. aquatica* (Micoletzky, 1913) Loos, 1948

syn. *Tylencholaimus aquaticus* Micoletzky, 1913

*Criconema aquaticum* (Micoletzky) Micoletzky, 1917

*Hoplolaimus aquaticus* (Micoletzky) Menzel, 1917

*Procriconema aquaticum* (Micoletzky) Micoletzky, 1925

*H. arcuata* Thorne, 1955

*H. arenaria* Raski, 1958

*H. argiensis* Khan & Nanjappa, 1972

*H. armandae* Banna & Gardner, 1993

*H. belemnitis* Germani & Luc, 1973

*H. biloculata* Colbran, 1969

*H. biosphaera* Chitambar, Mahato, McClure & Marino, 1997

*H. brevicauda* Sauer, 1958

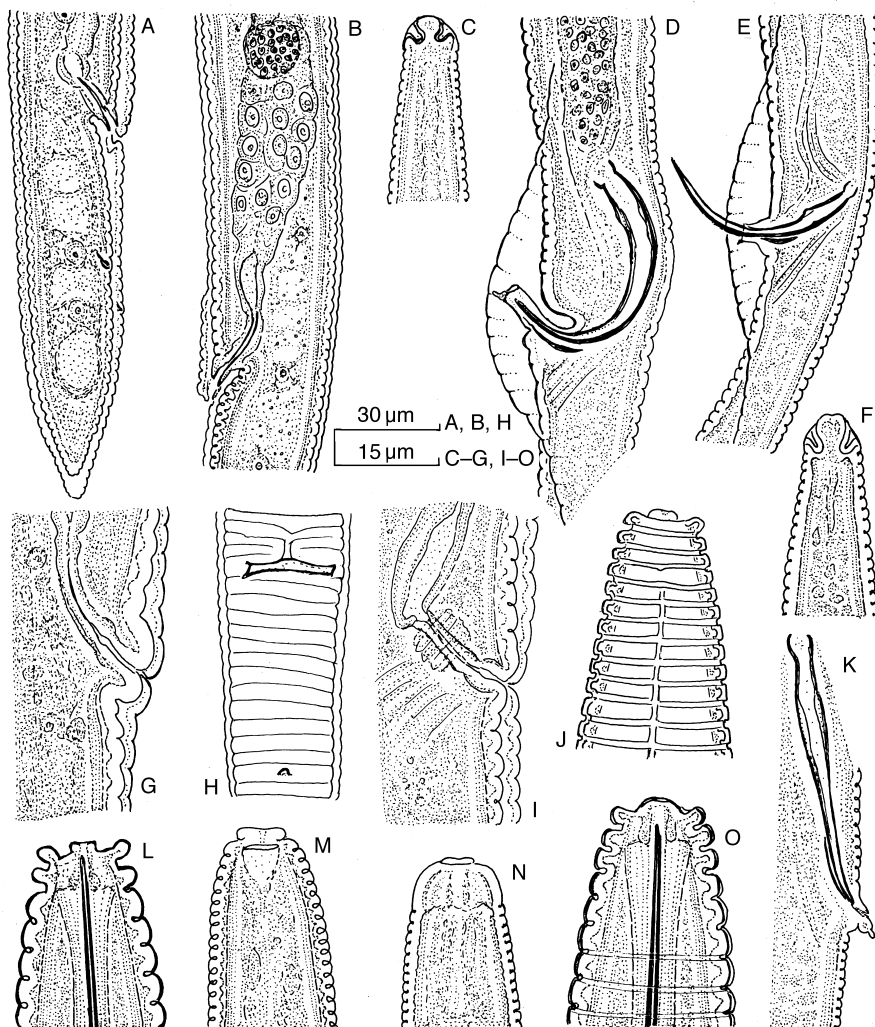
*H. brevis* Thorne, 1955

*H. californica* Brzeski, 1974

*H. catarinensis* Manso, 1996

*H. charlestoni* Reay, 1985

*H. chathamii* Yeates, 1978



**Fig. 126.** A. *Hemicycliophora epicharoides* Loof, paratype female, posterior region. B–D. *Hemicycliophora typica* de Man, from Holland. B. Vulval region. C. Male head end. D. Spicular region. E, F and I. *Loofia thienemanni* (Schneider), from Holland. E. Spicular region. F. Male head end. I. Vulval region. G and H. *Loofia robusta* (Thorne), paratype female, posterior region in lateral and ventral view, respectively. J. *Hemicaloosia delpradi* (Maas), paratype female, head end. K–M. *Caloosia paralongicaudata* (Siddiqi & Goodey), from Bangladesh. K. Spicular region. L. Female head end. M. Male head end. N. *Hemicaloosia paradoxa* (Luc), paratype male, head end. O. *Hemicaloosia nudata* (Colbran), paratype female, head end. (After Siddiqi (1980b), courtesy *Revue de Nématologie*.)

- syn. *Hemicycliophora chathamii chathamii* Yeates, 1978  
*Hemicycliophora chathamii major* Yeates, 1978
- H. chilensis* Brzeski, 1974  
 syn. *H. thienemanni* apud Andr ssy, 1967
- H. conida* Thorne, 1955
- H. corbetti* Siddiqi, 1980
- H. demani* Edward & Rai, 1971
- H. diolaensis* Germani & Luc, 1973
- H. ekdavici* Darekar & Khan, 1981 (syn. of *H. natalensis* for Costa-Manso, 1998)  
 syn. *Hemicycliophora veechi* Maqbool, Shahina & Zarina, 1986
- H. ekrami* Sultan & Singh, 1982
- H. epicharis* Raski, 1958
- H. epicharoides* Loof, 1968
- H. eucalypti* Reay, 1985
- H. eugeniae* Khan & Basir, 1963
- H. filicauda* Doucet, 1982
- H. floridensis* (Chitwood & Birchfield, 1957) Goodey, 1963  
 syn. *Hemicriconemoides floridensis* Chitwood & Birchfield, 1957  
*Hemicriconemoides biformis* Chitwood & Birchfield, 1957  
*Hemicycliophora biformis* (Chitwood & Birchfield) Goodey, 1963
- H. fluvialis* Bird, 1999
- H. fragilis* Doucet, 1982
- H. garhwalensis* Gupta & Gupta, 1982
- H. gracilis* Thorne, 1955
- H. guptai* Duggal & Kaul, 1985
- H. halophila* Yeates, 1967
- H. hellenica* Vovlas, 2000
- H. hesperis* Raski, 1958
- H. iberica* Castillo, Gomez-Barcina & Loof, 1989
- H. index* Jairajpuri & Khan, 1976
- H. iranica* Loof, 1984
- H. italiae* Brzeski & Ivanova, 1978
- H. iwia* Brzeski, 1974
- H. juglandis* Choi & Geraert, 1975
- H. koreana* Choi & Geraert, 1971
- H. labiata* Colbran, 1971  
 syn. *Hemicycliophora dhirendri* Husain & Khan, 1967
- H. lambertii* Van den Berg, 1988
- H. litoralis* Reay, 1985
- H. litorea* Van den Berg, 1987
- H. loofi* Maas, 1970
- H. lutosa* Loof & Heyns, 1969  
 syn. *Hemicycliophora lutosoides* Loof, 1984 (syn. by Costa-Manso, 1998)
- H. macristhmus* Loof, 1968
- H. macrodorata* Raski & Valenzuela-A., 1986
- H. madagascariensis* Germani & Luc, 1973
- H. mangiferae* Misra & Edward, 1971 (original spelling *mangiferum*)

- H. megalodiscus* Loof, 1984  
*H. mettleri* Jenkins & Reed, 1964  
*H. micoletzkyi* Goffart, 1951  
*H. minora* Wu, 1966  
*H. montana* Eroshenko, 1980  
*H. monticola* Mehta, Raski & Valenzuela, 1983  
*H. nana* Thorne, 1955  
*H. natalensis* Loof & Heyns, 1969  
*H. nigeriensis* Germani & Luc, 1973  
*H. nortoni* Brzeski, 1974  
*H. nucleata* Loof, 1968  
*H. nullinca* Van den Berg, 1987  
*H. nyanzae* Schoemaker, 1968  
*H. obesa* Thorne, 1955  
*H. obtusa* Thorne, 1955  
*H. ornamental* Bajaj, 1998  
*H. oryzae* De Waele & Van den Berg, 1988  
*H. ovata* Colbran, 1962  
*H. parajuglandis* Choi & Geraert, 1995  
*H. parvana* Tarjan, 1952  
*H. pauciannulata* Luc, 1958  
*H. peca* Van den Berg, 1987  
*H. pinocheti* Mehta & Raski, 1985  
*H. poranga* Monteiro & Lordello, 1978  
*H. postamphidia* Rahaman, Ahmad & Jairajpuri, 1996  
*H. pruni* Kirjanova & Shagalina, 1974  
*H. pseudochilensis* Barbez & Geraert, 1980  
*H. punensis* Darekar & Khan, 1981  
*H. quercea* Mehta & Raski, 1985  
*H. raskii* Brzeski, 1974  
*H. repetekensis* Krall, Ivanova & Shagalina, 1987  
*H. rionegrensis* Doucet, 1982  
*H. ripa* Van den Berg, 1981  
*H. ritteri* Brizuela, 1963  
*H. rotundicauda* Thorne, 1955  
*H. saueri* Brzeski, 1974  
*H. sculpturata* Loof, 1984  
*H. shepherdii* Wu, 1966  
*H. sheri* Brzeski, 1974  
*H. siddiqii* Deswal & Bajaj, 1987  
*H. signata* Orton Williams, 1978  
*H. similis* Thorne, 1955  
*H. spinituberculata* Loof, 1984  
*H. spinosa* Colbran, 1969  
*H. stiaani* Van den Berg & Tiedt, 1999  
*H. straturata* Germani & Luc, 1973  
*H. striatula* Thorne, 1955

- H. sturhani* Loof, 1984  
*H. subaolica* Jairajpuri & Baqri, 1973  
*H. tarjani* Khan & Basir, 1963  
*H. tenuis* Thorne, 1955  
*H. tenuistriata* Doucet, 1982  
*H. tessellata* Sauer, 1958  
*H. thornei* Goodey, 1963  
     syn. *Hemicycliophora typica* apud Thorne, 1955  
*H. transvaalensis* Heyns, 1962  
*H. triangulum* Loof, 1968  
*H. utkali* Ray & Das, 1981  
*H. vidua* Raski, 1958  
     syn. *Hemicycliophora silvestris* Jenkins & Reed, 1964  
     *Hemicycliophora vivida* Wu, 1966  
*H. vitiensis* Orton Williams, 1978  
*H. wallacei* Reay, 1985  
*H. wesca* Van den Berg & Meyer, 1987  
*H. zuckermani* Brzeski, 1963

#### Species incertae sedis

- Hemicycliophora lingualis* Kannan, 1961 (probably a species of *Hemicriconemoides*)  
*H. tessellata* Boonduang & Ratanaprapa, 1974 (= junior primary homonym of *H. tessellata* Sauer, 1958; now syn. of *Hemicaloosia paradoxa*)

ETYMOLOGY. From Greek *hemi* = half, *kyklos* = circle, *pherein* = to bear (semicircular spicule bearer).

The single male of the type species was collected by de Man in 1917 from a compost heap in the Municipal Park at Bergen-op-Zoom, The Netherlands.

#### Genus *Aulosphora* Siddiqi, 1980

syn. *Aulophora* apud Loof, 1985 (unjustified emendation)

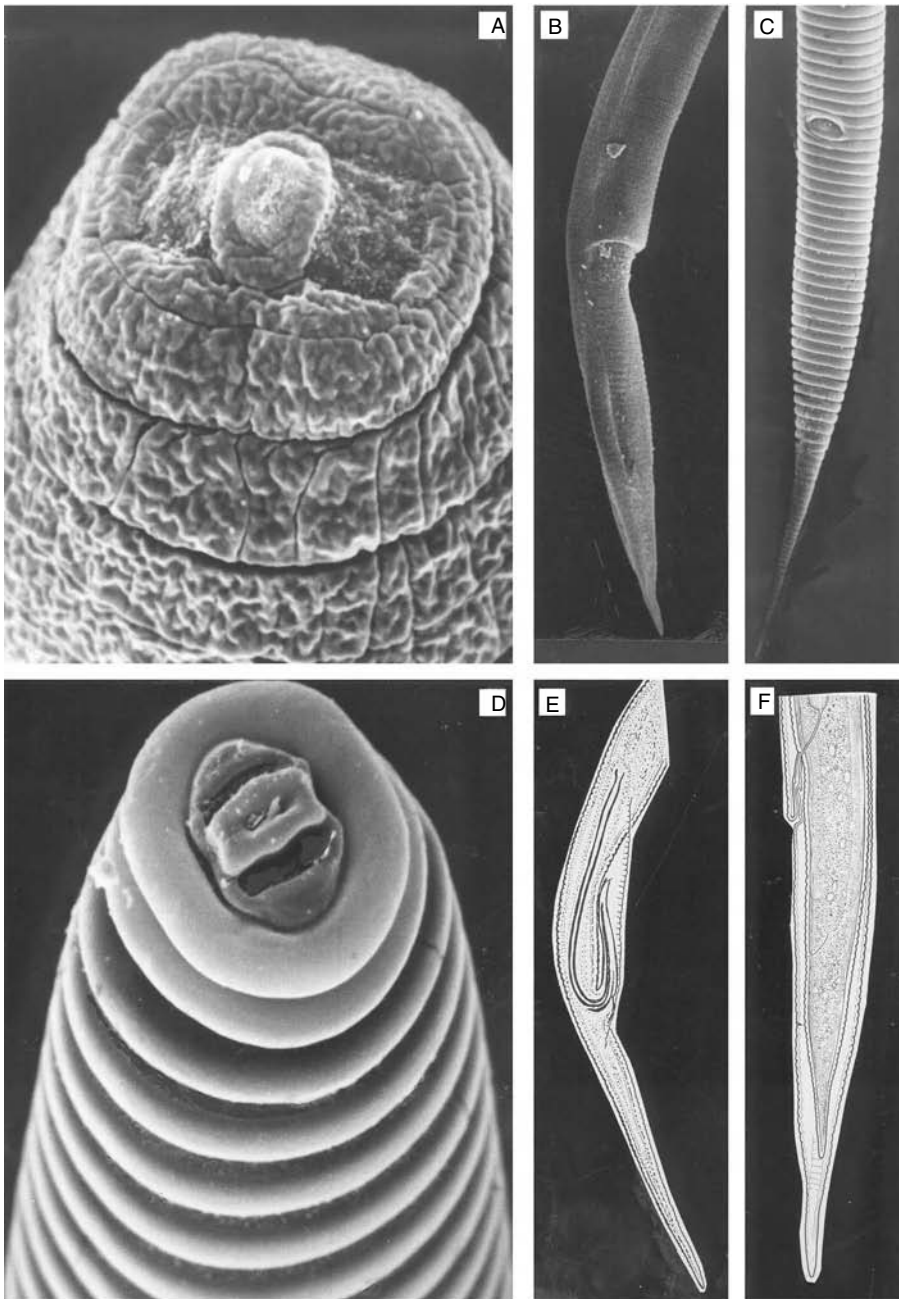
(Fig. 127, A, B, E & F)

#### Diagnosis

Hemicycliophorinae. Cephalic region broadly rounded, continuous with body. Body only slightly recessed behind vulva. Female and juvenile tails elongate-conoid, filiform. **Vulva lips elongate, tubular, over three body annules long, directed backward.** Spicules elongate-setaceous, U- or hook-shaped. **Penial tube longer than body width**, directed forward often touching ventral body surface; body not deeply recessed anterior to base of penial tube. **Pre- and postanal stretches of bursa in the ratio of 3–4:1.**

#### Type species

- Aulosphora penetrans* (Thorne, 1955) Siddiqi, 1980  
     syn. *Hemicycliophora penetrans* Thorne, 1955



**Fig. 127.** A, B, E and F. *Aulosphora* spp. C and D. Scanning electron micrographs of *Caloosia* sp. female from India. A and B. Scanning electron micrographs of face view and posterior region, respectively, of a female of *Aulosphora indica* (Siddiqi) from India. E. Male tail end of *Aulosphora penetrans* (Thorne). F. Female tail end of *Aulosphora indica* (Siddiqi).



## Other species

- Aulosphora attapadii* (Rahaman, Ahmad & Jairajpuri, 1996) comb. n.  
 syn. *Hemicycliophora attapadii* Rahaman, Ahmad & Jairajpuri, 1996
- A. bilineata* (Singh & Khan, 1999) comb. n.  
 syn. *Hemicycliophora bilineata* Singh & Khan, 1999 (original spelling *bilineatus*)
- A. brzeskii* (Barbez & Geraert, 1980) Siddiqi, 1980  
 syn. *Hemicycliophora brzeskii* Barbez & Geraert, 1980
- A. dahomensis* (Germani & Luc, 1976) Siddiqi, 1980  
 syn. *Hemicycliophora dahomensis* Germani & Luc, 1976
- A. indica* (Siddiqi, 1961) Siddiqi, 1980  
 syn. *Hemicycliophora indica* Siddiqi, 1961  
*Hemicycliophora musae* Khan & Nanjappa, 1972  
*Aulosphora musae* (Khan & Nanjappa) Siddiqi, 1986
- A. karachiensis* Maqbool, Shahina & Zarina, 1986 (syn. of *Hemicycliophora typica* for Costa-Manso, 1998)  
 syn. *Aulosphora karachiensis* Maqbool, Shahina & Zarina, 1986 (*Aulosphora* unjustified emendation for *Aulosphora*)
- A. meghalayaensis* (Rahaman, Ahmad & Jairajpuri, 1996) comb. n.  
 syn. *Hemicycliophora meghalayaensis* Rahaman, Ahmad & Jairajpuri, 1996
- A. oostenbrinki* (Luc, 1958) Siddiqi, 1980  
 syn. *Hemicycliophora oostenbrinki* Luc, 1958
- A. osmani* (Das & Shivaswamy, 1977) Siddiqi, 1980  
 syn. *Hemicycliophora osmani* Das & Shivaswamy, 1977
- A. paracouensis* (Van den Berg & Quénéhervé, 1995) comb. n.  
 syn. *Hemicycliophora paracouensis* Van den Berg & Quénéhervé, 1995

ETYMOLOGY. From Greek *aulos* = tube (refers to penial tube), and *pherein* = to bear.

The type species was described on specimens collected from rice and maize plots at Bogor, Java, Indonesia. A key to species was given by Siddiqi (1980).

**Genus *Colbranium* Andrásy, 1979**

(Fig. 125, N)

## Diagnosis

Hemicycliophorinae. Female cephalic region set off by a deep groove, tail short, rounded. **Vulva and anus close together, subterminally located in a ventral depression of body.** Vulva lips not modified, low, rounded. Spicules arcuate but not semicircular. Penial tube well developed but less than body width long, directed outward and forward. **Bursa subterminal.**

## Type species

- Colbranium truncatum* (Colbran, 1956) Andrásy, 1979  
 syn. *Hemicycliophora truncata* Colbran, 1956

No other species.

ETYMOLOGY. Patronym honouring R.C. Colbran, Queensland, Australia.

The type species was collected from around the roots of *Chloris gayana* Kunth (Rhodes grass) at Archerfield, Queensland, Australia.

### Genus *Loofia* Siddiqi, 1980

(Fig. 126, E–I)

#### Diagnosis

Hemicycliophorinae. **Female cephalic region conoid**, continuous. Body behind vulva not conspicuously recessed. Female and juvenile tails elongate-tapering to filiform. **Vulva lips rounded**, not modified or raised. **Spicules arcuate**, not semicircular. Penial tube not well developed, less than three body annules long; body anterior to base of penial tube not recessed. Pre- and postanal stretches of bursa almost equal.

#### Type species

*Loofia thienemanni* (Schneider, 1925) Siddiqi, 1980  
 syn. *Hoplolaimus thienemanni* Schneider, 1925  
*Hemicycliophora thienemanni* (Schneider) Loos, 1948  
*Procriconema thienemanni* (Schneider) Micoletzky, 1925  
*Hemicycliophora salicis* Sofrygina, 1972  
*Loofia salicis* (Sofrygina, 1972) comb. n.

#### Other species

*Loofia acuta* Reay, 1985  
*L. gigas* (Thorne, 1955) Siddiqi, 1980  
 syn. *Hemicycliophora gigas* Thorne, 1955  
*L. planiannulata* (Singh & Khan, 1999) comb. n.  
 syn. *Hemicycliophora planiannulata* Singh & Khan, 1999 (original spelling *planiannulatum*)  
*L. robusta* (Loof, 1968) Siddiqi, 1980  
 syn. *Hemicycliophora robusta* Loof, 1968  
*L. uniformis* (Thorne, 1955) Siddiqi, 1980  
 syn. *Hemicycliophora uniformis* Thorne, 1955  
*Hemicycliophora ferrisae* Brzeski, 1974 (syn. by Costa-Manso, 1998)  
*Loofia ferrisae* (Brzeski, 1974) Siddiqi, 1980  
*L. vaccinii* (Reed & Jenkins, 1963) Siddiqi, 1980  
 syn. *Hemicycliophora vaccinii* Reed & Jenkins, 1963 (original spelling *vaccinia*)

#### Note

*Aulosphora* and *Loofia* are based on the structure of the genital organs of females and males, which are strong generic characters because the genital organs change little during evolution since they must be compatible during copulation and this has a great significance in species evolution.

ETYMOLOGY. Patronym honouring P.A.A. Loof.

The type habitat and locality for the type species is moist soil, Alfsburg Island, Lake Ploner, East Holstein, Germany. A key to species was given by Siddiqi (1980b).

## FAMILY CALOOSIIDAE

*Caloosia* and *Hemicaloosia* spp. (family Caloosidae) occur widely in eastern and southern India and in Sri Lanka. *Caloosia exilis* was collected from rhizospheres of 38 plant species in Orissa State, India, where *C. heterocephalus* and *C. triannulata* occurred in rice and pineapple soils, respectively (Ray & Das, 1981). *Caloosia paxi* and *C. parapaxi* were described from mango soil in Assam, India. *Caloosia heterocephalus* fed on meristematic tissues of rice roots continuously for 3–4 h, the oesophageal bulb pulsating 55–136 (average 83) times per min, with intermissions of 10–30 min (Rao & Mohandas, 1976).

Members of Caloosiidae lack sheathed juveniles, the unique characteristic of the Hemicycliophoridae. This characteristic alone provides a firm basis to recognize Caloosiidae as a family.

### Family Caloosiidae Siddiqi, 1980

#### Diagnosis

Hemicycliophoroidea. Large-sized with elongate filiform tails, male tail shorter than that of female, with a large bursa covering more than one-third of tail. **Females and juveniles either lack a body sheath or have a membranous sheath** being much thinner than the body cuticle and closely adpressed to it; lateral fields present only in forms with a sheath. Cephalic annules separated and usually modified in juveniles and females. Male cephalic region continuous with body, lacking lateral 'spectacle mark'. Vulva transversely oval, less than half body width long, partially overhung by its dorsal lip, thus appearing flush with body contour. **Vagina sigmoid. Spicules straight**; cloacal lips not elongated to form a penial tube.

#### Type subfamily

Caloosiinae Siddiqi, 1980

No other subfamily

### Subfamily Caloosiinae Siddiqi, 1980

#### Diagnosis

Caloosiidae, with characters of the family.

#### Type genus

*Caloosia* Siddiqi & Goodey, 1964

#### Other genus

*Hemicaloosia* Ray & Das, 1978

### Key to genera of Caloosiinae

1. Females and juveniles with a body sheath and lateral fields ..... *Hemicaloosia*  
Females and juveniles without a body sheath and lateral fields ..... *Caloosia*

### Genus *Caloosia* Siddiqi & Goodey, 1964

(Figs 126, K–M; 127, C & D)

#### Diagnosis

Caloosiinae. Female 0.85–1.06 mm and male 0.74–0.82 mm long in type species. **Body sheath and lateral fields in females and juveniles absent.** Annules contiguous with folded cuticle in between. Stylet 74–92  $\mu\text{m}$  long in female and spicules 42–45  $\mu\text{m}$  long in type species. Cephalic region of male annulated, not marked off from body by discontinued annulation.

#### Type species

*Caloosia longicaudata* (Loos, 1948) Siddiqi & Goodey, 1964  
syn. *Hemicycliophora longicaudata* Loos, 1948

#### Other species

*Caloosia brevicaudata* Khan, Chawla & Saha, 1979  
*C. exilis* Mathur, Khan, Nand & Prasad, 1969  
syn. *Caloosia indica* Chawla & Samathanam, 1980  
*C. paralongicaudata* Siddiqi & Goodey, 1964  
syn. *Hemicycliophora longicaudata* apud Siddiqi, 1961  
*C. parlonga* Khan, Chawla & Saha, 1979  
*C. paxi* Mathur, Khan, Nand & Prasad, 1969  
syn. *Caloosia heterocephalus* Rao & Mohandas, 1976 (original spelling *heterocephala*)  
*Caloosia parapaxi* Phukan & Sanwal, 1980  
*C. peculiaris* Van den Berg & Meyer, 1991  
*C. psidii* Gambhir & Dhanachand, 1997  
*C. shorai* Gambhir & Dhanachand, 1997  
*C. triannulata* Ray & Das, 1981

ETYMOLOGY. Patronym honouring Clive A. Loos.

The type species was described by Loos (1948) from Sri Lanka (Ceylon), possibly from forest soil. A key to species was given by Ganguly & Khan (1983).

### Genus *Hemicaloosia* Ray & Das, 1978

(Fig. 126, J, N & O)

#### Diagnosis

Caloosiinae. Female 0.74–0.84 mm and male 0.61–0.66 mm long in type species. **A membranous body sheath and lateral fields in females and juveniles present.** Annules usually separated by grooves, cuticle not folded between annules. Lateral field on body sheath marked by two incisures. Female stylet 60–64  $\mu\text{m}$  long and spicules 33–36  $\mu\text{m}$  long in type species. Cephalic region of male smooth, marked off from body by a discontinuity in annulation.

## Type species

*Hemicaloosia americanae* Ray & Das, 1978 (original spelling *americana*)  
syn. *Caloosia americanae* (Ray & Das) Raski & Luc, 1987

## Other species

*Hemicaloosia delpradi* (Maas, 1970) Siddiqi, 1980  
syn. *Caloosia delpradi* Maas, 1970  
*H. luci* Dhanachand & Jairajpuri, 1980  
syn. *Caloosia luci* (Dhanachand & Jairajpuri) Raski & Luc, 1987  
*H. nudata* (Colbran, 1963) Ray & Das, 1978  
syn. *Hemicycliophora nudata* Colbran, 1963  
*Caloosia nudata* (Colbran) Brzeski, 1974  
*H. paradoxa* (Luc, 1958) Ray & Das, 1978  
syn. *Hemicycliophora paradoxa* Luc, 1958  
*Caloosia paradoxa* (Luc) Brzeski, 1974

ETYMOLOGY. Derived from the prefix of *Hemicycliophora*, and *Caloosia*.

The type species was collected from rhizosphere of *Agave americana* L. at Madhujhari, Phulbani district, Orissa State, India.

## **SUPERFAMILY TYLENCHULOIDEA SKARBILOVICH, 1947 (RASKI & SIDDIQUI, 1975)**

**syn. Tylenchulidoidea Raski & Siddiqui, 1975 (= incorrect spelling)  
Tylenchocriconematoidea Raski & Siddiqui, 1975**

## Diagnosis

Criconematina. **Body small (rarely over 0.5 mm), becoming obese in females of several genera. Cuticle thin, finely annulated** (secondarily thickened and without discernible annulation in obese females), lateral field with two to four incisures, may occasionally be obscure. **Female:** Lip region smooth lacking prominent annules, continuous with body, with or without submedian lobes. Postcorpus large, muscular, amalgamated with broad precorpus, which may be slender in short-stylet forms. **Isthmus slender**, not amalgamated with basal bulb which is usually small and rounded; oesophageal glands free in body cavity only in *Tumiota*. Vulva a large transverse slit. Ovary outstretched, or coiled in obese females. Uterine wall thick in obese females, may form a cystoid body in *Meloidoderita*. Excretory cell may be abnormally enlarged to produce a gelatinous matrix in which eggs are deposited (e.g. *Tylenchulus*). **Male:** Oesophagus degenerated and stylet degenerate or absent. Bursa usually absent, if present low, adanal to subterminal (enveloping entire tail in *Tylenchocriconema*). Spicules setose, arcuate, with pointed tip. Hypoptygma single, usually absent. **Gonoduct packed with minute sperm; testis in adult degenerates;** the entire complement of sperm is probably produced just before the final moult. **Juveniles:** Similar to female in most details, but some juveniles lack a stylet. Ectoparasites (rarely secondarily obese females becoming endoparasites) of roots.

## Type family

Tylenchulidae Skarbilovich, 1947

## Other families

Paratylenchidae Thorne, 1947

Sphaeronematidae Raski & Sher, 1952

**Key to families of Tylenchuloidea**

1. Stylet long (usually over 20  $\mu\text{m}$  and with conus abnormally elongated);  
precorpus broad; female usually vermiform, if saccate, then body elongate obese,  
enlarging on all sides; males and juveniles usually strongly curving ventrally upon  
relaxation, with short tails ..... **Paratylenchidae**  
Stylet short (usually under 15  $\mu\text{m}$  and with conus not abnormally elongated);  
precorpus slender; female subspherical to spherical, or elongate-obese with body  
enlarging mostly dorsally; males and juveniles usually not curving upon  
relaxation, with elongate tails ..... **2**
2. Adult female spherical or subspherical, lacking a postvulval region; excretory  
pore in oesophageal region ..... **Sphaeronematidae**  
Adult female not spherical or subspherical, with a distinct postvulval region;  
excretory pore much behind oesophageal region (except *Boomerangia*)  
..... **Tylenchulidae**

**FAMILY TYLENCHULIDAE****(Criconematina with small stylet and obese, curved females)**

*Tylenchulus semipenetrans*, the citrus root nematode, is one of the most important plant parasites. The nematode is an obligate, highly specialized parasite of citrus throughout the world. It causes a disease called 'slow decline' which affects most citriculture and results in poor growth and vigour of trees, yellowing and shedding of leaves, undersized fruits and a marked crop loss. Certain strains or pathotypes attack grapevines, loquat, persimmon and olive. Infested vineyards in Victoria (Australia) showed a general unthriftiness which was cured by reducing the nematode populations by fumigation (Sauer, 1962).

The eggs are deposited often in batches of 10–20 in a gelatinous matrix produced by the excretory system through the excretory pore (cf. *Meloidogyne* and *Heterodera*, in which the matrix is produced through the anus and vulva, respectively). The eggs hatch in 12–14 days at 24°C, the first moult occurring within the egg. The second-stage juvenile develops to maturity within 7 days without feeding. The egg-to-egg life cycle is completed in 6–10 weeks. The juveniles can survive more than a month without food. The nematode remains in the soil for several years after the tree is felled, feeding and multiplying on the roots.

The citrus root nematode buries its anterior region into the root, several cortical cells deep, and establishes a feeding site, which includes six to ten cortical cells grouped around the nematode head and modified to form the so-called 'nurse cells'. The nurse cells are like the giant cells produced by members of the Meloidogynidae

or Heteroderidae. The nematode feeds on these cells and its posterior part begins to swell while remaining exposed to the environment.

The nematode is usually spread by citrus nurseries since the seedlings and root-stocks are carried to virgin soil 'balled' with infested soil. Bare-root dips in hot water (at 45°C for 25 min) and in suitable concentrations of nematicides can control the spread of disease (see review by Siddiqi, 1974).

Phylogenetically, the citrus root nematode is one of the many small-sized, thin-cuticled and short stylet-bearing Criconematina showing a highly specialized root parasitism (for more details see under Sphaeronematidae). Allen (1960) pointed out that the family Tylenchulidae, then comprised of *Tylenchulus*, *Trophotylenchulus*, *Trophonema* and *Sphaeronema*, was more closely related to the Paratylenchinae than to any group in the Tylenchida, and that due to various differences these genera should be better placed in a separate family than with the Paratylenchinae or the Criconematidae. He argued that *Sphaeronema*, with a spherical female lacking a tail and having thick cuticle and broken annules, might be considered to represent the most specialized of the four genera of the family. Of these, *Sphaeronema* merits a separate family, Sphaeronematidae, to which also belong the genera *Goodeyella* Siddiqi, 1986, *Meloidoderita* and *Tumiota* Siddiqi, 1986.

Skarbilovich (1947) proposed the subfamily as Tylenchululinae, and Kirjanova (1955) recognized it as a family. Raski (1957) also proposed the family Tylenchulidae and considered under it two subfamilies, Tylenchulinae (with *Tylenchulus* and *Trophotylenchulus*) and Sphaeronematinae (with *Sphaeronema* and *Trophonema*). Maggenti (1962) proposed the synonymy of *Trophotylenchulus* with *Tylenchulus*. Raski & Siddiqui (1975), raising Tylenchulidae to superfamily, mistakenly called it Tylenchulidoidea. Geraert (1966) elevated Sphaeronematinae to family and assigned Sphaeronematidae and Tylenchulidae to the Criconematoidea.

Siddiqi (1980b, 1983a) believed that the Tylenchuloidea represented a separate evolutionary line from that of the Criconematoidea and Hemicycliophoroidea, and that it showed various parasitic adaptations (obesity of body, initiation of nurse or transfer cells in root tissues, etc.) and differed from the latter groups in having a thin cuticle and slender isthmus offset from the basal bulb, the members of the two lines sharing a common ancestor and representing a natural group, the Criconematina (more details under Sphaeronematidae).

## **Family Tylenchulidae Skarbilovich, 1947 (Kirjanova, 1955)** **syn. Tylenchulidae Raski, 1957**

### **Diagnosis**

Tylenchuloidea. Small nematodes (under 0.5 mm), with **marked sexual dimorphism in body form and anterior region**; female obese, with well-developed stylet and oesophagus; male slender, with degenerate stylet and oesophagus. Cuticle thin (except in obese females), finely annulated. Lateral fields present (obscure in obese females). **Female: Elongate-obese, ventrally curved, with a distinct postvulval region.** Cephalic region rounded, with or without perioral elevation. **Stylet about 15 µm or shorter**; knobs rounded. Orifice of dorsal gland one-third to one-half stylet length behind stylet base. Basal bulb enclosing gland, offset from isthmus and intestine. **Excretory pore generally well behind oesophagus; excretory cell (renette)**

**enormously developed, producing gelatinous matrix.** Vulva a large transverse slit. Postvulval uterine sac absent. Uterus with thick walls, and only one mature egg at a time. **No uterine cyst formed.** Ovary coiled in obese females. Eggs laid in gelatinous matrix. Anus generally rudimentary or absent. **Tail present,** short. **Male:** Body almost straight when relaxed. Cephalic region rounded, continuous. Stylet reduced or absent. Testis outstretched, degenerate in adult; gonoduct paced with minute, rounded sperm. Spicules small, slender, arcuate, cephalated. **Juveniles:** Slender, **straight to arcuate when relaxed.** Deirids often present. Stylet well developed, 15  $\mu\text{m}$  or shorter. Precorpus and isthmus elongate-slender. Excretory pore generally much posterior to oesophagus. Tail elongate-conoid, minutely rounded. Obligate ectoparasites of roots; female sedentary with swollen body almost always remaining outside roots.

#### Type subfamily

Tylenchulinae Skarbilovich, 1947

No other subfamily.

### **Subfamily Tylenchulinae Skarbilovich, 1947** **syn. Tylenchululinae Skarbilovich, 1947** **(= incorrect original spelling)**

#### Diagnosis

Tylenchulidae. With characters of the family.

#### Type genus

*Tylenchulus* Cobb, 1913

#### Other genera

*Boomerangia* Siddiqi, 1991

*Trophotylenchulus* Raski, 1957

#### **Key to genera of Tylenchulinae**

(based on female)

1. Excretory pore in female at 68–85% of body length, surrounded by papilla-like outgrowths ..... *Tylenchulus*  
 Excretory pore in female at less than 61% of body length, not surrounded by outgrowths ..... 2
2. Female body arcuate, slightly swollen ..... *Boomerangia*  
 Female body spirally coiled; considerably swollen ..... *Trophotylenchulus*

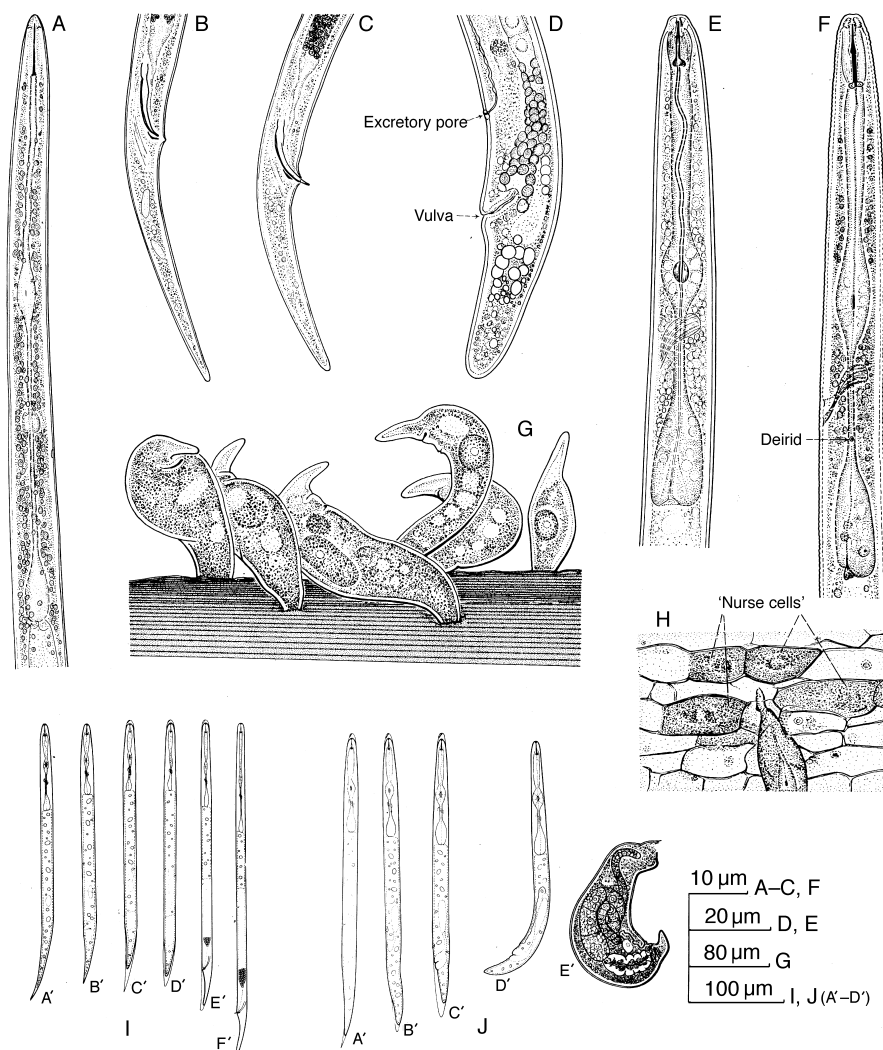
#### **Genus *Tylenchulus* Cobb, 1913**

(Fig. 128)

#### Diagnosis

Tylenchulinae. Preadult female migratory, adult female sedentary. Male non-feeding. **Mature female:** Elongate-obese, enlarging behind median bulb, mostly on dorsal





**Fig. 128.** *Tylenchulus semipenetrans* Cobb. A. Oesophageal region of male. B and C. Male tails. D and E. Tail end and oesophageal region of immature female from Brookville, Florida (USA), respectively. F. Oesophageal region of second-stage juvenile. G. Females on citrus root from Brookville, Florida (USA). H. Feeding site of a female showing 'nurse cells'. I and J. Developmental stages of male and female, respectively. (D, E, G and J (E')) Redrawn from pencil sketches made by N.A. Cobb. I(A'–F') and J(A'–D'). After Van Gundy (1958), remainder after Siddiqi (1974).)

side, **ventrally arcuate**, not spiral; neck elongate, irregular in outline; **postvulval part elongate-tapering**; maximum width up to 100  $\mu\text{m}$ . Cuticle 3–5  $\mu\text{m}$  thick near middle. Stylet 11–15  $\mu\text{m}$  long, knobs prominent. Excretory system well developed, **produces gelatinous matrix**; renette cell occupying about 30% of body cavity in type species. **Excretory pore** 12–19  $\mu\text{m}$  in front of vulva at 68–85% of body length

from anterior end; **papilla-like outgrowths around excretory pore present.** Excretory duct leading inward and forward. Isthmus elongate slender. Basal bulb offset from intestine. Intestine syncytial, lacking a lumen. Vulva a distinct transverse slit, lips bulging. Postvulval uterine sac absent. Spermatheca present. Ovary coiled, or with one to two flexures, extending to oesophageal region. **Anus obscure or absent, non-functional.** Tail tapering, tip rounded or with a peg. **Immature female:** Vermiform, slender, straight to arcuate upon relaxation. Cuticle distinctly striated. Stylet and oesophagus as in mature female. Excretory pore at 76–84% of body length in type species. Vulva lips thick, bulging. Ovary immature, with a few oocytes. Anus obscure. **Male:** Slender, straight or slightly arcuate ventrally, 0.33–0.46 mm long. Stylet and oesophagus degenerate but not completely. Excretory pore at 53–60% of body length. Testis outstretched. Spicules slender, arcuate, 14–20  $\mu\text{m}$  long. Gubernaculum simple, fixed, 3–6  $\mu\text{m}$  long. **Bursa absent.** Penial tube not formed. Tail elongate-conoid, tip rounded or with a peg. **Second-stage juvenile:** Slender, straight to slightly arcuate when relaxed. Lateral fields narrow, each with two incisures. **Deirids present,** just behind nerve ring. Excretory pore at 50–60% of body length; excretory duct leading from pore inward and forward. Cephalic region rounded; labial disc indistinct; framework moderately sclerotized. Stylet 11–15  $\mu\text{m}$  long, knobs rounded. Orifice of dorsal gland 3–5  $\mu\text{m}$  behind stylet base. Median bulb oval or fusiform, with elongated refractive thickenings. Basal bulb offset from isthmus and intestine. Rectum and anus obscure. Tail elongate-conoid, tip rounded (type species) or deeply furcate (*T. furcus*). No uterine cyst formed. Female fixed into the root by its anterior part. **Feeding on root induces nurse cells of the same size as normal cortical cells but with hypertrophied nuclei and dense cytoplasm. A capsule-like structure surrounding adults and juveniles absent.**

#### Type species

*Tylenchulus semipenetrans* Cobb, 1913

#### Other species

*Tylenchulus furcus* Van den Berg & Spaull, 1982

*Tylenchulus graminis* Inserra, Vovlas, O'Bannon & Esser, 1988

*Tylenchulus palustris* Inserra, Vovlas, O'Bannon & Esser, 1988

ETYMOLOGY. Latin diminutive of *Tylenchus*.

The type species was described from citrus roots from Brookville, Florida, USA (see Siddiqi, 1974). *Tylenchulus furcus* parasitizes sugarcane and grass in South Africa.

#### Genus *Trophotylenchulus* Raski, 1957

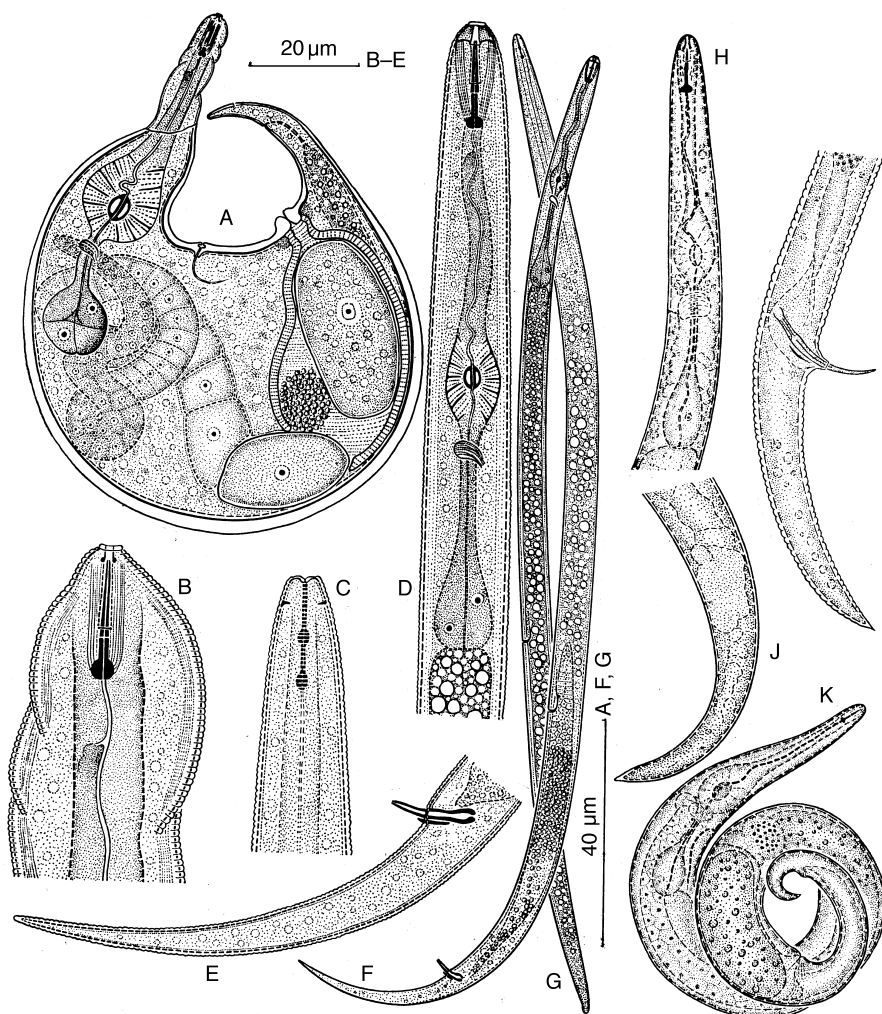
syn. *Ivotylenchulus* Hashim, 1984

*Trophonema* Raski, 1957

(Fig. 129)

#### Diagnosis

Tylenchulinae. Body small (females and juveniles about 0.38–0.48 mm). Cuticle thin, finely annulated; female lateral fields obscure. **Female elongate-saccate,**



**Fig. 129.** A–G. *Trophotylenchulus manganoti* (Luc). H–K. *Trophotylenchulus arenarius* (Raski). A and K. Females. B. Head end of female. C. Head end of male. D and H. Oesophageal regions of juveniles. E and I. Tail ends of males. F. Male. G. Juvenile. J. Tail end of juvenile. (A–G. After Luc (1957), courtesy *Nematologica*. H–K. After Raski (1956), courtesy Helminthological Society of Washington.)

coiled curving more than 360°; postvulval body region remaining slender. Juveniles slender, vermiform, straight to arcuate on death. Cephalic region of female and juveniles continuous, anteriorly tapering, usually surmounted by a distinct circumoral elevation or disc (= fused submedian lobes). Excretory pore located near nerve ring or behind oesophageal base, at 33–61% of body length from anterior end; papilla-like outgrowths around excretory pore absent (cf. *Tylenchulus*). Excretory cell (renette) enormously developed, located laterally,

**produces gelatinous matrix.** Stylet well developed, usually 11–15  $\mu\text{m}$  long; knobs prominent, spheroid. Orifice of dorsal gland about half stylet length behind stylet base. Stylet and oesophagus in male degenerate. Precorpus elongate-slender. Median bulb large, with prominent refractive thickenings. Isthmus slender. Basal bulb pyriform, enclosing oesophageal glands. Ovary extending anteriorly, with flexures. Postvulval uterine sac absent, but slightly indicated in mature females. Tails in all stages elongate-conoid to a rounded terminus. Spicules arcuate with ventrally bent tip, 13–20  $\mu\text{m}$  long. Cloacal lips raised; single hypopygium present. Bursa absent. Females fixed into root by anterior part only; **feeding on root induces syncytium with hypertrophied nuclei and dense cytoplasm. Adult females usually encapsulated in a round, capsule-like structure apparently produced by host reaction.**

#### Type species

- Trophotylenchulus floridensis* Raski, 1957  
syn. *Tylenchulus floridensis* (Raski) Maggenti, 1962

#### Other species

- Trophotylenchulus andhraensis* Muthukrishnan & Shariff, 1986  
*T. arenarius* (Raski, 1956) Siddiqi, 1999  
syn. *Sphaeronema arenarium* Raski, 1956  
*Trophonema arenarium* (Raski) Raski, 1957  
*Paratylenchus arenarius* (Raski) Geraert, 1966  
*T. arthemidis* Dolinski, Souza & Huang, 1996  
*T. asoensis* (Minagawa, 1983) Siddiqi, 1999  
syn. *Trophonema asoense* Minagawa, 1983 (syn. of *T. arenarium* for Gomez-Barcina & Castillo, 1990)  
*T. clavicaudatus* (Colbran, 1966) Cohn & Kaplan, 1983  
syn. *Tylenchulus clavicaudatus* Colbran, 1966  
*Trophotylenchulus clavicaudatus* (Colbran) Hashim, 1984  
*T. colbrani* Siddiqi, 1999  
*T. cunctus* Siddiqi, 1999  
*T. manganoti* (Luc, 1957) Goodey, 1963  
syn. *Tylenchulus manganoti* Luc, 1957  
*Ivotylenchulus manganoti* (Luc) Hashim, 1984  
*T. obscurus* (Colbran, 1961) Cohn & Kaplan, 1983  
syn. *Tylenchulus obscurus* Colbran, 1961  
*Trophotylenchulus obscurus* (Colbran) Hashim, 1984  
*T. okamotoi* (Minagawa, 1983) Siddiqi, 1999  
syn. *Trophonema okamotoi* Minagawa, 1983 (syn. of *T. arenarium* for Gomez-Barcina & Castillo, 1990)  
*T. piperis* Mohandas, Ramana & Raski, 1985  
*T. saltensis* Hashim, 1984  
*T. waliai* Bajaj & Bhatti, 1990

#### Notes

Luc (1957) illustrated a gubernaculum protruded along with the spicule and, on the basis of his illustration, Hashim (1984) used the character of the gubernaculum as

'apparently protrusible through the cloacal aperture'. In some cases, the gubernaculum is pushed out with the spicular protrusion but it remains within the distended body or rectal lining. Luc (1957) pointed out that, in contrast to *Tylenchulus semipenetrans*, *Trophotylenchulus floridensis* and *Trophonema arenarium*, *Tylenchulus manganoti* has a functional anus. Raski & Luc (1987) considered the character of the protrusible gubernaculum and the absence of a spicular sheath of *Ivotylenchulus* as not having sufficient significance to justify a separate generic taxon and synonymized the genus with *Trophotylenchulus*. *Trophonema* Raski, 1957 differs from *Trophotylenchulus* Raski, 1957 in the female body shape and the anterior position of the excretory pore. Siddiqi (1999) described *T. cunctus* Siddiqi, 1999, which had a body curvature typical of *Trophotylenchulus* but the excretory pore was located in the oesophageal region. He considered the position of the excretory pore as a variable character in the genus and synonymized *Trophonema* Raski, 1957 with *Trophotylenchulus* Raski, 1957, which has page priority over the former. *Trophonema asoense* Minagawa, 1983 and *Trophonema okamotoi* Minagawa, 1983 were considered junior synonyms of *T. arenarium* by Gomez-Barcina & Castillo (1990) because they were differentiated on the tail shape of the swollen females. Inserra *et al.* (1993) considered them as valid species.

ETYMOLOGY. From Greek *trophos* = one who feeds or *trophis* = swollen, and *Tylenchulus*.

*Trophotylenchulus floridensis* was found parasitizing roots of *Quercus falcata*, *Magnolia* sp. and *Diospyros* sp. in Florida, USA. *Trophotylenchulus piperis* occurs on black pepper (*Piper nigrum* L.) in Kerala, India. As the females of *T. floridensis* and *T. piperis* feed and mature, they develop a protective covering which later turns brown. In *T. piperis* it is initiated as a transparent jelly, probably produced by the excretory system of the nematode. The protective case starts developing in 30–40 days after inoculation and eggs are laid inside it, number of eggs per case ranging from 25 to 35 for *T. piperis*, the life cycle from egg to egg taking up to 55 days at 24–32°C (Sundararaj *et al.*, 1995). *Trophotylenchulus clavicaudatus* and *T. obscurus* occur in Queensland, Australia and *T. saltensis* on *Olea europaea* in Jordan. The latter species has also been reported to occur in Cameroon, Kenya and South Africa. *Trophotylenchulus manganoti* was found parasitizing roots and rhizomes of *Dorstenia embergeri* G. Manganot (family Moraceae) at Abidjan, Côte d'Ivoire. *Trophotylenchulus colbrani* and *T. cunctus* were described from the Mbalmayo forest reserve in Cameroon. The females of *T. floridensis* were partially embedded in the roots and occurred singly in small, two cells thick, darkened galls. *Trophotylenchulus arenarius* parasitizes roots of *Juncus leseurii* Boland in California, USA. The females occur on roots as ectoparasites and do not form colonies. They are found coiled in a gelatinous matrix in association with eggs and coiled juveniles. *Trophotylenchulus okamotoi* feeds on cortical tissue of sweet gum roots in Florida, inciting syncytia in the cortex (Inserra *et al.*, 1993). In contrast, *Sphaeronema ramicis* and *Meloidoderita* sp., which also produce syncytia, are stelar feeders and *Tylenchulus* spp. incite formation of clusters of nurse cells. The gelatinous matrix in these tylenchs is produced by the excretory–secretory system which is enormously developed.

### Genus *Boomerangia* Siddiqi, 1991

(Fig. 130)

#### Diagnosis

Tylenchulinae. Juveniles, male and preadult female vermiform, straight to slightly arcuate upon fixation; adult mature female slightly swollen near middle and appears boomerang-like when relaxed; less than 0.5 mm long. **Marked sexual dimorphism in anterior region, with stylet and oesophagus of male degenerate.** Cuticle thin, finely striated. Lateral field, deirid and phasmid not seen. Cephalic region conoid-rounded, continuous, smooth, with indistinct oral disc; framework sclerotized. Stylet of female and juvenile well developed; female stylet short (under 20  $\mu\text{m}$ ) but strong; conus sharply pointed, about half of total stylet length; knobs rounded. Orifice of dorsal oesophageal gland 4–6  $\mu\text{m}$  behind stylet in type species. Median oesophageal bulb oval, strongly muscular. Basal oesophageal bulb pyriform, offset from intestine. **Excretory pore opposite isthmus or basal bulb;** excretory canal leading inward and backward. Vulva at about 70% of body length. Ovary single, anteriorly outstretched. **Postvulval uterine sac absent.** Spermatheca rounded, with small rounded sperm in type species. Crustaformeria apparently a tricolumella but cells not in rows. Rectum short, indistinct. Anus pore-like, indistinct. Tails similar between sexes, elongate-conoid to a small rounded terminus, slightly ventrally arcuate; **hyaline region at terminus inconspicuous.** Spicules ventrally arcuate, cephalated, pointed. Gubernaculum small, fixed. Bursa absent.

#### Type species

*Boomerangia benigna* Siddiqi, 1994

#### Other species

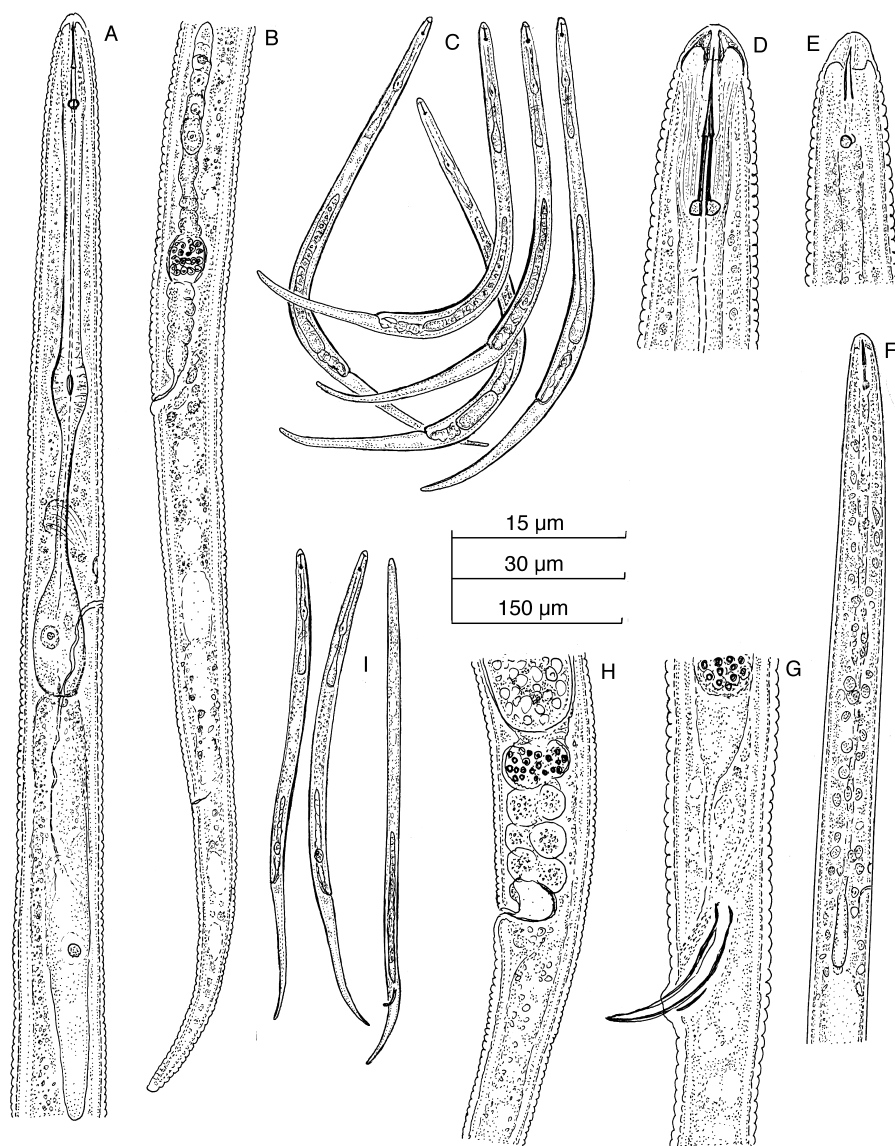
*Boomerangia bellula* Siddiqi, 1994

ETYMOLOGY. Generic name is derived from boomerang-like shape of mature female body upon relaxation. The genus is feminine in gender.

The type species was found in soil around roots of a forest tree, *Palisota* sp., in Korup National Park, near Mundemba town, Ndian Division, South-West Province, Cameroon. *Boomerangia bellula* was also found in the same locality.

## FAMILY SPHAERONEMATIDAE (Criconematina with round to lemon-shaped females)

Members of this family show the highest degree of adaptation to plant parasitism among the suborder Criconematina. They perhaps share a common ancestor with forms such as *Paratylenchus* and *Tylenchulus*, one that is supposed to have a small body size, thin cuticle with or without very fine annulation, a narrow rounded cephalic region, small stylet, weakly developed oesophagus and elongate tail. The family contains four genera and only 12 species are known so far. The juveniles and males are vermiform but the female undergoes changes to become swollen and



**Fig. 130.** *Boomerangia benigna* Siddiqi. A and B. Immature female, anterior and posterior regions, respectively. C. Mature females. D. Head end of mature female. E. Head end of male. F. Oesophageal region of male. G. Spicular region. H. Vulval region. I. Two immature females and a male. (A–I. After Siddiqi (1994), courtesy *Afro-Asian Journal of Nematology*.)

attains the status of a most successful root parasite, despite such restraints as minuteness of body and thin cuticle.

**1. Self-preservation.** The juveniles are slender and active and are provided with a well-developed feeding stylet and oesophagus. They attack and feed on roots

ectoparasitically, penetrating into the deeper tissues. The female develops to maturity at a suitable feeding site and induces the formation of specialized feeding cells in the form of a syncytium involving the pericycle and phloem cells of the root, which look different from those produced by *Tylenchulus semipenetrans*. The anchorage to plant tissues is obtained by the variously modified neck region. The postneck region of the body swells to become subspherical or spherical with the terminal shifting of the vulva and thus resulting in disappearance of the entire postvulval region, including the superfluous tail (no longer needed in a sedentary mode of life). Most of the body thus transforms into a spheroidal sac containing the feeding and reproductive organs and the cuticle becomes several times thicker.

**2. Race preservation.** The stylet and oesophageal pump are strongly developed for continuous feeding. Even the median bulb becomes spherical to lose its criconematid nature! The lumen of the oesophagus is very distinct, opening into the intestine, which is obliterated into an open space around the reproductive organs. The uterus grows to almost fill the body cavity. Perhaps it provides surfaces for food absorption. The eggs are laid singly (not in groups) in a gelatinous matrix or retained in an enlarged uterine cystoid body (*Meloidoderita*). When the body is small (about 100  $\mu\text{m}$ ) only a single egg can be retained in the uterus (*Goodeyella*), but in large-sized forms several eggs are packed in it (*Tumiota*).

Females of *Sphaeronema californicum* were found inside the roots of *Umbellularia californica* and the nematode occurred in colonies. *Goodeyella minutissima* females were found on the surface of the roots with their necks buried deep into the tissue. *Meloidoderita kirjanovae* is a sedentary ectoparasite of *Mentha longifolia* (L.) in Armenia and Israel and *Meloidoderita polygona* parasitizes several species of *Polygonum* in the USA. *Meloidoderita* spp. also occur in the Azores, Iran, Germany and South Africa.

## Family Sphaeronematidae Raski & Sher, 1952 (Geraert, 1966) syn. Meloidoderitidae Kirjanova & Poghossian, 1973

### Diagnosis

Tylenchuloidea. Small to moderate sized (0.1–0.7 mm). **Marked sexual dimorphism present.** Adult female spherical or subspherical with or without neck. Male with degenerate oesophagus and no stylet. Juveniles and female with well-developed oesophagus and stylet and **excretory pore located in oesophageal region.** **Female:** Cuticle thick with indistinct or no annulation. Cephalic region small, elevated, sclerotization delicate. **Stylet 15  $\mu\text{m}$  or shorter (rarely up to 27  $\mu\text{m}$ ); conus equal to or slightly longer than shaft,** knobs rounded. Oesophagus with cylindrical precorpus, spheroidal muscular postcorpus, **a slender isthmus** and usually a small basal bulb containing glands, or rarely with glands enlarged and extending over intestine. **Vulva a transverse slit, terminal,** on a protuberance of body or flush with body surface. **Uterus swells to form a thick-walled chamber** which may fill most of the body cavity. **Ovary coiled. Tail absent.** **Male:** Gonoduct filled with small round sperm, testis degenerate in adult. Female a sedentary ectoparasite. Tail conoid. Bursa absent. Spicules slightly arcuate. Cloacal lips conoid, may be slightly elongated. **Juveniles:** Vermiform. Cephalic region continuous, elevated,



sclerotization pyriform, containing glands which may extend over intestine in *Tumiota*. Stylet stout, less than 15  $\mu\text{m}$  long, with round basal knobs. Tail elongate-conoid to small rounded terminus. Females of *Goodeyella* and *Sphaeronema* are sedentary endoparasites of roots, the only known instances of endoparasitism among Criconematina.

#### Type subfamily

*Sphaeronematinae* Raski & Sher, 1952

#### Other subfamily

*Meloidoderitinae* Kirjanova & Poghossian, 1973

### Key to subfamilies of Sphaeronematidae

1. Adult female with a neck; uterine walls do not form a protective cystoid body for eggs ..... **Sphaeronematinae**  
 Adult female without a neck; uterine walls form a protective cystoid body for eggs ..... **Meloidoderitinae**

### Subfamily Sphaeronematinae Raski & Sher, 1952

#### Diagnosis

*Sphaeronematidae*. Adult female spherical, subspherical or lemon-shaped, **with a slender neck** variously modified by root tissues. Vulva flush with body contour or on a cone-like protuberance. **Uterus** thick-walled, contains one or more eggs at a time, but **not filling the entire body cavity or turning into a cystoid body**; eggs laid in a gelatinous matrix.

#### Type genus

*Sphaeronema* Raski & Sher, 1952

#### Other genera

*Goodeyella* Siddiqi, 1986

*Tumiota* Siddiqi, 1986

### Key to genera of Sphaeronematinae

1. Mature female with vulva on a cone-like protuberance of body ..... ***Sphaeronema***  
 Mature female with vulva flush with body surface ..... **2**
2. Female and juveniles with oesophageal glands enclosed in basal bulb; juvenile cephalic region with a truncate circumoral elevation ..... ***Goodeyella***  
 Females and juveniles with oesophageal glands extending over intestine; juvenile cephalic region rounded ..... ***Tumiota***

**Genus *Sphaeronema* Raski & Sher, 1952**

(Fig. 131)

**Diagnosis**

Sphaeronematinae. **Mature female:** Subspherical (0.13–0.21 mm long). **Cuticle** up to 9  $\mu\text{m}$  thick, **marked by a well-defined reticulate pattern**. Lateral fields not marked by definite lines. Cephalic sclerotization delicate. Stylet 14–20  $\mu\text{m}$  long, conus 58–60% of stylet length, basal knobs well developed, rounded, slightly sloping posteriorly. Dorsal gland orifice 4–5  $\mu\text{m}$  behind stylet. Median bulb rounded, with prominent refractive thickenings. Posterior bulb pyriform, well set off from slender isthmus. Oesophago-intestinal junction and intestine obscure. Anus and tail absent. **Excretory pore opposite or near median bulb. Vulva cleft-like, terminal, on a cone-like protuberance of body**, with small cuticular lateral membranes. Immature female nematodes pear-shaped, lacking reticulate cuticular pattern and vulva protuberance. Eggs laid in a gelatinous matrix. **Male:** Vermiform, 0.39–0.47 mm long. Oesophagus degenerate. Cephalic region smoothly rounded, slightly offset. Stylet absent. Spicules slender, slightly arcuate and cephalated, 19–21  $\mu\text{m}$  long. Gubernaculum simple, 3–4  $\mu\text{m}$  long. Cloacal lips form a short penial tube. Bursa absent. Tail elongate-conoid, pointed. **Juveniles:** Body as long as that in males. Cuticle finely and indistinctly annulated. Cephalic region continuous, rounded, sclerotization moderate. Stylet 13–23  $\mu\text{m}$ , conus 53–57% of stylet length, knobs round. Postcorpus muscular, merging anteriorly with precorpus. Isthmus slender, basal bulb pyriform, offset from intestine. **Excretory pore in isthmus region**. Tail arcuate, tapering into a bluntly rounded tip, anus obscure. Female an obligate parasite of plant root.

**Type species**

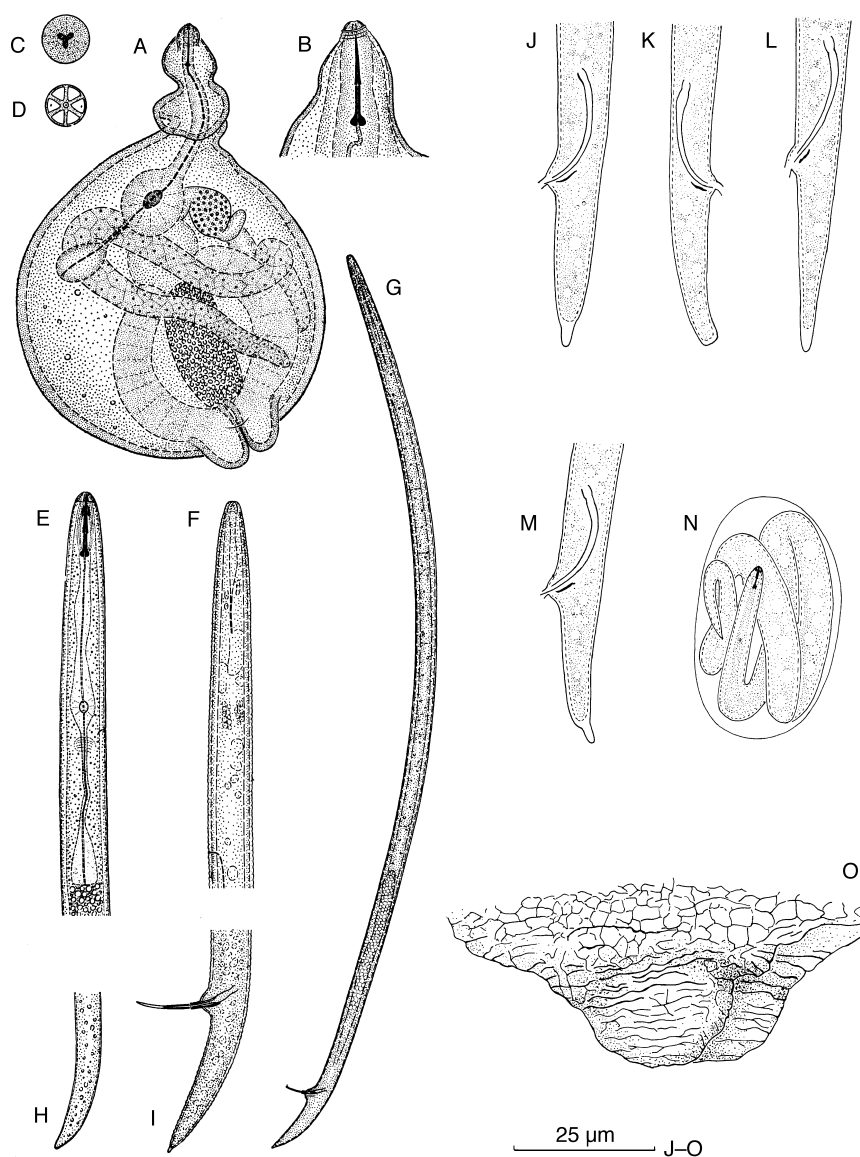
*Sphaeronema californicum* Raski & Sher, 1952

**Other species**

- Sphaeronema alni* Turkina & Chizhov, 1986
- S. camelliae* Aihara, 1985
- S. cornubiense* Van den Berg & Spaull, 1982
- S. rumicis* Kirjanova, 1970
- S. salicis* Eroshenko, 1989
- S. sasseri* Eisenback & Hartman, 1985

ETYMOLOGY. From Greek *sphaira* = globe, and *nema* = nematode.

The type species was found parasitizing Californian laurel, *Umbellularia californica*, in California, USA.



**Fig. 131.** *Sphaeronema californicum* Raski & Sher. A. Mature female. B and O. Anterior and posterior regions of mature female, respectively. C. Cross-section of median oesophageal bulb. D. En face view. E and H. Anterior and posterior regions of juvenile, respectively. F. Anterior region of male. G. Male. I-M. Tail regions of male. N. Fully developed juvenile inside egg. (A-I. After Raski and Sher (1952), courtesy Helminthological Society of Washington. J-O. After Machon (1975).)

**Genus *Goodeyella* Siddiqi, 1986**

(Fig. 132, A–E)

**Diagnosis**

Sphaeronematinae. Extremely small nematodes (female: 0.1–0.13 mm long, about 66  $\mu\text{m}$  wide; juveniles 0.296–0.338 mm long in type species). **Female:** **Body almost spherical**, with a neck. Cuticle thick and smooth with no markings. **Cephalic region with a circumoral, truncate elevation**, cuticle just behind this elevation thickened slightly. Stylet almost 8  $\mu\text{m}$  long (seen in one female), with prominent knobs. Postcorporate bulb almost spherical, isthmus short, expanding to a small spatulate basal bulb containing three glands which may be located within spherical region of body. Intestine obliterated, the space within spherical body filled mostly with enlarged uterus and reproductive organs. **Vulva terminal, flush with body surface**. Vagina short, thick-walled. **Uterus thick-walled, spherical, containing an almost spherical egg** (shape of uterus and egg possibly determined by the body shape). **Ovary short and broad, with few oocytes**. Male not known. **Juveniles:** Vermiform. Cuticular annules fine, 0.7  $\mu\text{m}$  wide. Lateral field and anus obscure. **Cephalic region** smooth, continuous, **tapering to a circumoral truncate elevation** as in female. Stylet 12–13  $\mu\text{m}$  long, conus slightly longer than the shaft, basal knobs with convex anterior and flattened posterior surfaces. Orifice of dorsal gland 4–5  $\mu\text{m}$  behind stylet base. Oesophagus about a quarter of total body length, with refractive thickenings at about its middle. Tail elongate-conoid to a small round terminus.

**Type species**

*Goodeyella minutissima* (Goodey, 1958) Siddiqi, 1986

syn. *Sphaeronema minutissimum* Goodey, 1958

No other species.

ETYMOLOGY. Generic name is a patronym honouring J.B. Goodey, who found this nematode and foresaw a new genus for it.

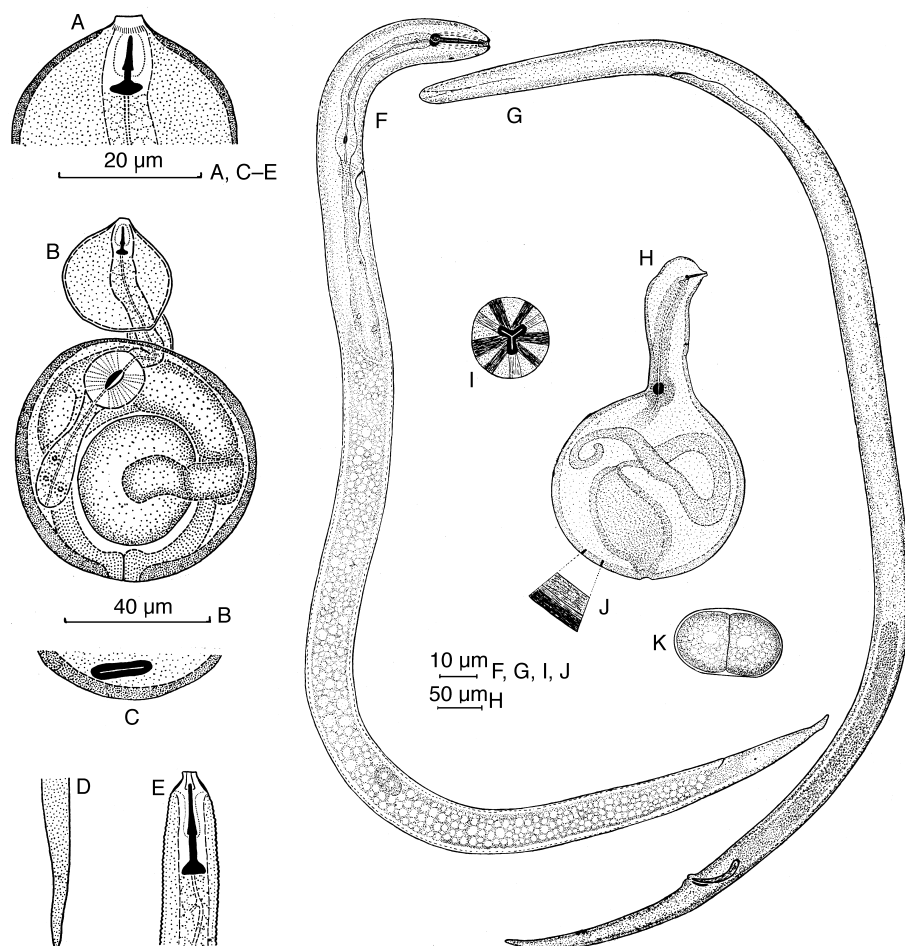
The type species was found on *Citrus* sp. from Pasar Minggu near Djakarta, Indonesia.

**Genus *Tumiota* Siddiqi, 1986**

(Fig. 132, F–K)

**Diagnosis**

Sphaeronematinae. Small to medium-sized (0.33–0.65 mm), juveniles and males vermiform, females swollen, with spheroid body. **Female:** **Body spherical to sub-spherical with protruding neck**. Cephalic region elevated, sclerotization delicate. Stylet 19–21  $\mu\text{m}$  long, with conus 54–57% of total stylet length, basal knobs rounded. Orifice of dorsal gland 3–4  $\mu\text{m}$  behind stylet base. Precorpus elongate-cylindrical, postcorpus spheroidal, very muscular, with refractive thickenings. Uterus thick-walled, **in mature females distended and packed with eggs**. **Vulva terminal, flush with body surface, lips not protruding**. Eggs 75–80  $\mu\text{m}$  long, 45–50  $\mu\text{m}$  wide. **Male:** Body 0.39–0.47 mm long, slender ( $a = 32$ –39). Cephalic region



**Fig. 132.** A–E. *Goodeyella minutissima* (Goodey). F–K. *Tumiota whittoni* (Sledge & Christie). A. Head end of female. B and H. Females. C. Vulva in surface view. D. Tail end of juvenile. E. Head end of juvenile. F. Juvenile. G. Male. I. Cross-section of median oesophageal bulb of female. J. Enlarged section of cuticle. K. Egg. (A–E. After Goodey (1958). F–K. After Sledge & Christie (1962), courtesy *Nematologica*.)

smooth, continuous. Lateral fields obscure, oesophagus degenerate, stylet absent, testis single, gonoduct packed with hundreds of small round sperm. Spicules arcuate, pointed, 12–14  $\mu\text{m}$  long. Gubernaculum simple, trough-like, 5–6  $\mu\text{m}$  long. Bursa absent. Tail conoid, with small round tip, slightly arcuate. **Second-stage juvenile:** 0.4–0.48 mm long. Stylet about 19  $\mu\text{m}$  long, with conus 47–65% of stylet length and round basal knobs. Cuticle finely annulated. **Cephalic region continuous, rounded**, with weak sclerotization. Orifice of dorsal gland about 3  $\mu\text{m}$  behind stylet base. Median oesophageal bulb elongate, with refractive thickenings. Isthmus well defined. **Oesophageal glands extending over intestine.** Anus obscure. Tail tapering to finely rounded terminus.

### Type species

*Tumiota whittoni* (Sledge & Christie, 1962) comb. n.

syn. *Sphaeronema whittoni* Sledge & Christie, 1962

No other species.

ETYMOLOGY. Latin *tumeo* = to swell, *iota* = smallest Greek letter (for small size, a particle).

The type species was found on roots of sweetgum (*Liquidambar styraciflua* L.) at the bank of Hatchet Creek, 8 miles east of Gainesville, Florida, USA.

## Subfamily Meloidoderitinae Kirjanova & Poghossian, 1973

### Diagnosis

Sphaeronematidae. Adult female spheroidal or lemon-shaped, **lacking a neck**. Vulva on a terminal cone-like elevation of body; anus shifted to dorsal side. Uterus thick-walled, fills most of body cavity, in older females **uterus transforms into a cystoid body**, serving as protective sac for the retained eggs; some eggs retained, others laid in a gelatinous matrix.

### Type genus

*Meloidoderita* Poghossian, 1966

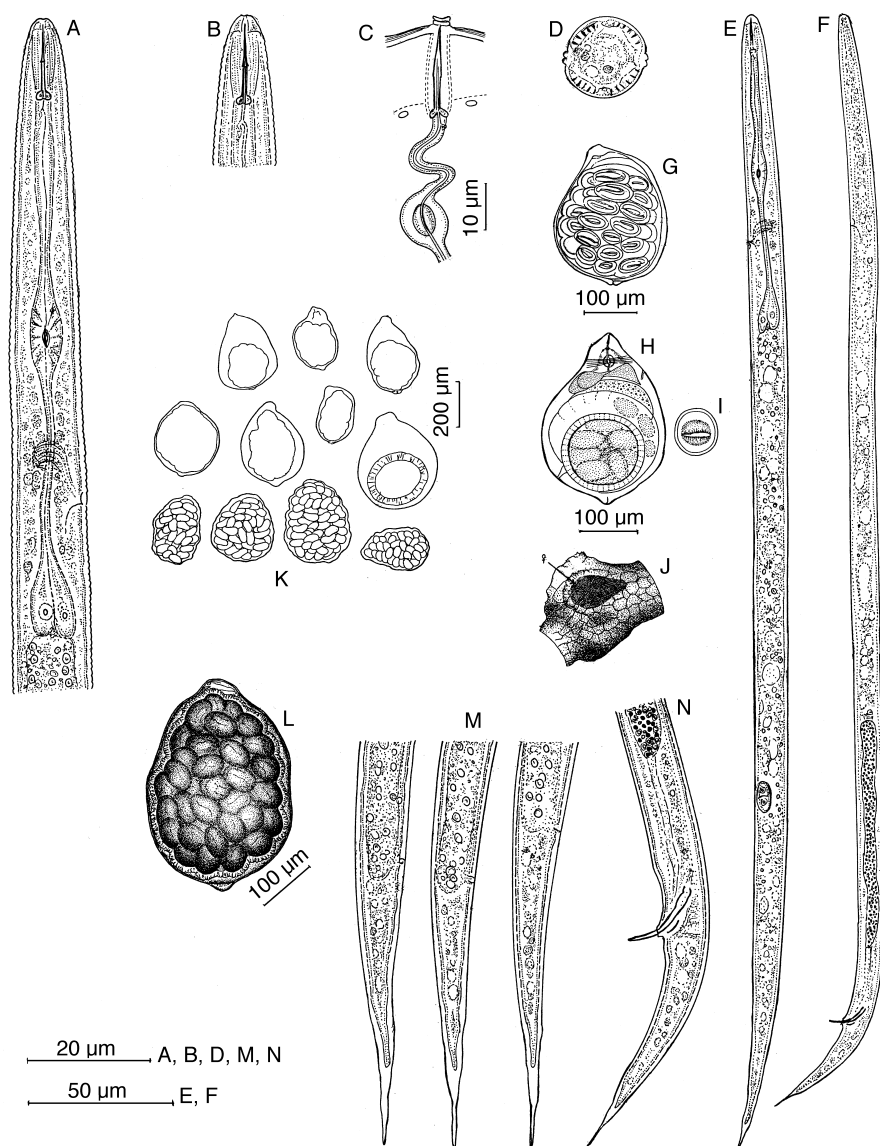
No other genus.

### Genus *Meloidoderita* Poghossian, 1966

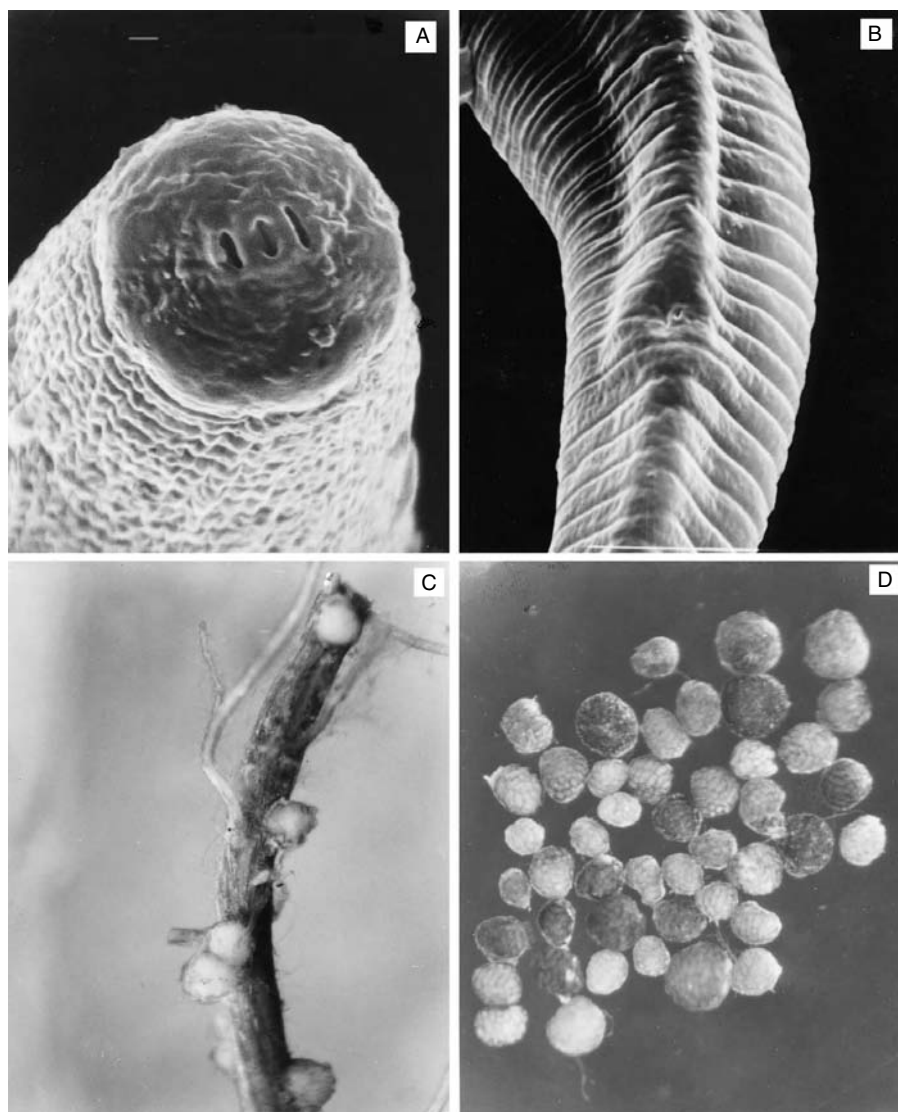
(Figs 133 & 134)

### Diagnosis

Meloidoderitinae. Small-sized (under 0.5 mm). Marked sexual dimorphism. **Mature female: Body fully swollen, without a neck or tail**, pear-shaped or oval, 0.21–0.45 mm long, 0.14–0.37 mm wide in type species. **Vulva terminal, on a cone-like elevation of body**. Longitudinal axis of body from head to vulva; anus shifted to dorsal side 44–180  $\mu\text{m}$  from vulva in type species. Cuticle thick, may have spine-like outgrowths. Stylet about 15–19  $\mu\text{m}$  long, knobs prominent. Orifice of dorsal gland 3–7  $\mu\text{m}$  from stylet base. Excretory pore opposite median bulb; latter very muscular with large refractive thickenings. Uterus spheroidal, with very thick walls, filling one-third to a half of body cavity in young and **most of body in old females**. In old females uterus becomes patchily sclerotized with a palmate branched surface pattern and transforms into a **cystoid body**, 0.18–0.36 mm long and 0.15–0.35 mm wide in type species. Maternal body-wall withers off and the cystoid body serves as protecting case for the retained eggs. Several eggs are laid in gelatinous material which covers the females and, subsequently, the cystoid bodies. Eggs 60–92  $\mu\text{m}$  long, 35–50  $\mu\text{m}$  wide. **Male:** Slender, vermiform, under 0.5 mm long. Cephalic region continuous. Stylet absent. Oesophagus degenerate. Vas deferens packed with minute sperm, testis atrophied in mature males. Tail elongate, subcylindrical or conoid. Bursa absent. Spicules and gubernaculum typical of the family. **Second-stage juveniles:** Very similar to those of *Sphaeronema* spp., 0.31–0.44 mm



**Fig. 133.** A–E and G–M. *Meloidoderita kirjanovae* Poghossian, from *Mentha* sp. root and soil in Armenia. F and N. *Meloidoderita* sp. from *Mentha* sp. soil in Israel. A and B. Second-stage juvenile head ends. C. Female head and stylet. D. Cross-section of body of second-stage juvenile. E. Second-stage juvenile. F. Male. G, H and L. Mature females. I. Vulva in ventral view. J. Female in root. K. Developmental stages of cystoid body through uterine enlargement. M. Tail ends of second-stage juveniles. N. Tail end of male. (G. After Poghossian (1966). H–L. After Kirjanova and Poghossian (1973). Remainder after Siddiqi (1986).)



**Fig. 134.** *Meloidoderita polygona* Golden & Handoo. A. Scanning electron micrograph of head (*en face*) view of second-stage juvenile. B. Scanning electron micrograph of anal region of second-stage juvenile, ventral view (note pore-like anus). C. Females on root. D. Cystoid bodies. (A–D. Courtesy A.M. Golden and *Journal of Nematology*.)

long in type species, straight to arcuate upon relaxation. Cuticle finely annulated; lateral field with three or four incisures. Cephalic region conoid-rounded to truncate, continuous; labial disc indistinct; framework lightly sclerotized. Stylet well developed, 12–14  $\mu\text{m}$  long in type species; conus often a little longer than the shaft; knobs large, rounded. Median bulb oval, with prominent refractive thickenings. Isthmus long, slender. Oesophageal glands enclosed in terminal bulb, offset from or



with base slightly extending over intestine. Excretory pore opposite isthmus. Rectum and anus indistinct. Tail tip spicate, or minutely rounded.

#### Type species

*Meloidoderita kirjanovae* Poghossian, 1966

#### Other species

*Meloidoderita polygoni* Golden & Handoo, 1984

*Meloidoderita safrica* Van den Berg & Spaull, 1982

ETYMOLOGY. Diminutive of *Meloidodera*, to which it was thought to be related.

*Meloidoderita kirjanovae* was described from roots of *Mentha longifolia* (L.) Huds. from Armenia, where it also parasitizes *Mentha arvensis* and *Urtica dioica*. It is known from *Mentha* spp. from Uzbekistan, and northern Israel. *Meloidoderita safrica* is known to parasitize sugarcane in South Africa. *Meloidoderita polygoni* parasitizes species of Polygoniaceae in USA, completing its life cycle in 23 days at 31°C on *Polygonum hydropiperoides*. The second-stage juveniles penetrate roots and move through the cortex to feed on pericycle cells (Golden & Handoo, 1984).

## FAMILY PARATYLENCHIDAE (The pin nematodes)

This family is comprised of thin cuticle- and long stylet-bearing Criconematina which are generally very small (0.18–0.6 mm). Their cuticle is finely annulated and lateral fields are present in the female. The stylet has a conus longer than the shaft and spheroidal basal knobs. It is often extremely long, due mainly to the enlargement of the conus, and may become one-third or more of body length (*Cacopaurus* and *Gracilacus*). Feeding with this long stylet for long periods at one site often makes mature females enlarge on all sides and they may become sausage-shaped (*Cacopaurus*), but there are no spheroidal forms (cf. Sphaeronematidae).

The pin nematodes are extremely small and, although they occur in large numbers, easily go undetected. They are obligate root ectoparasites of a large variety of plants, shrubs and trees. They are especially common in orchard soils, reaching enormous numbers, as many as 250,000 *Paratylenchus* per litre of soil (Corbett, 1978). *Paratylenchus neoamblycephalus* occurs on apple, apricot, peach and on herbaceous plants in Australia, Europe and the Americas. Under unfavourable conditions, its fourth-stage juveniles do not moult, and become the survival stage, recognizable in having the stylet reduced or absent and oesophagus degenerated. The final moult occurs when conditions are favourable and there is stimulus from host root diffusates (Fisher, 1967).

The relatively short-stylet forms feed on root epidermal cells but the long-stylet *Gracilacus* spp. feed deep in the cortical tissue. *Paratylenchus neoamblycephalus* feeds on Myrobalan plum roots with its head buried deep in the root cortex. Inoculated plum seedlings had smaller, darker and reduced root systems and poor growth (Braun & Lownsbey, 1975). Low populations (650 nematodes per 100 cc soil) of *P.*

*hamatus* on rose improved flower production and quality, but high populations (2000 per 100 cc soil) reduced production as well as quality (MacDonald, 1976). *Paratylenchus pemoxius* is pathogenic to sorghum and needs high soil temperature (32–36°C) and moisture levels for its reproduction and is able to enter anhydrobiosis (Baujard & Martiny, 1994).

*Paratylenchus* (*Gracilacus*) *epacris* was implicated in a disease of California black walnut (*Juglans hindsii* Jepson) in California, USA (Allen & Jensen, 1950). *Paratylenchus* (*Gracilacus*) *capitatus*, found in large numbers on dying oak (*Quercus coccinea* Muench) in Virginia (USA), may be as important a pest to oaks as is *Cacopaurus* to walnuts (Adams & Eichenmuller, 1962). In the roots of the redwood tree (*Sequoia sempervirens*), *P.* (*Gracilacus*) *hamicaudatus* forms colonies under the cortex and lays eggs with a gelatinous matrix to protect them. It incites giant feeding cells in the parenchyma of the vascular tissue and, like *Cacopaurus pestis*, has a stylet in the fourth-stage juveniles.

*Cacopaurus pestis*, the sole representative of the genus, parasitizes *Juglans regia* in California, USA. It occurs in southern France on *Rosa indica major* L. and on *Citrus aurantium* L. and in Spain on *Syringa vulgaris* L. Males, which do not feed, and juveniles occur in soil; females are permanently attached to their feeding sites. Small colonies of nematodes, extending 1–3 cm along the root axis, are formed on walnut roots: more than 100 females were recovered from 1 g of rose roots.

Raski (1975a) gave a key to 48 species of *Paratylenchus* having a stylet less than 38 µm in length, and pointed out their small size and variation in the morphological characters. Yet he was able to distinguish between the species by using differences in body size, head and tail shapes, stylet length, number of incisures in the lateral fields and male characteristics, especially the degree of degeneration of the male stylet. Because of the importance of male characters in species differentiation, he proposed the male as holotype for his two new species *P. baldacci* and *P. ciccaronei*.

The genus *Gracilacus*, differentiated from *Paratylenchus* on the basis of the stylet length and position of the excretory pore, was synonymized with the latter genus by Siddiqi & Goodey (1964). This action was followed by Geraert (1965), Allen & Sher (1967) and Solovyova (1972) but was not accepted by Thorne & Malek (1968), Golden (1971) and Andrassy (1976). Raski (1976) reviewed *Gracilacus*, held it as valid, and stated that, in the obesity of the females, it was closer to *Cacopaurus* than to *Paratylenchus*. Members of this family form a coherent group but the differentiation of the genera assigned to it is often difficult. *Gracilacus* Raski, 1962 is not sufficiently different from *Paratylenchus*, but the two genera have been considered by many taxonomists as distinct. The males of the species of these groups do not show differentiating characters even at generic level.

Brzeski (1998) re-synonymized *Gracilacus* with *Paratylenchus* and argued that the difference between the shortest stylet of *Gracilacus* and the longest of *Paratylenchus* was 3 µm, which was not sufficient for the separation of genera, and that the position of the excretory pore relative to body length was constant at 18–28% of body length in both genera. Slight swelling of the body in mature females of *Paratylenchus* spp. having a stylet as small as 15 µm has been observed by me. *Gracilacus* was regarded as a subgenus of *Paratylenchus* by Siddiqi (1986) and is treated so in this edition.

Raski & Siddiqi (1975) proposed a new superfamily, Tylenchocriconematoidea

(the longest superfamily name in Tylenchida!) for *Tylenchocriconema alleni* and stated that it was intermediate between and related to both the Tylenchoidea and Criconematoidea, the tylenchoid features considered were the long caudal alae in the male and fine body annulation and elongate isthmus in the female and the criconematoid characters being the shape of the female corpus and the degenerate oesophagus of the male. *Tylenchocriconema alleni* fits the general family concept of the Paratylenchidae, and hence a separate superfamily or family for it is not justified. Raski & Luc (1987) recognized the subfamilies Tylenchocriconematinae and Paratylenchinae under the family Tylenchulidae.

## Family Paratylenchidae Thorne, 1949 (Raski, 1962) syn. Tylenchocriconematidae Raski & Siddiqui, 1975

### Diagnosis

Tylenchuloidea. **Vermiform, curving ventrally when relaxed**, plump, under 0.5 mm (except *Tylenchocriconema*), adult female if swollen remains cylindroid and vermiform. **Cuticle thin**, finely or moderately annulated. Lateral fields present, with incisures. Female and most juveniles with well-developed stylet and oesophagus, males with degenerate oesophagus and degenerate or no stylet. **Female:** Stylet well developed; conus abnormally elongated, often more than twice as long as shaft; knobs small, rounded. Oesophagus with a broad corpus having well-developed muscular postcorpus, a **slender isthmus**, a small offset basal bulb containing oesophageal glands. Excretory pore in oesophageal region; renette cell not abnormally enlarged. Vulva a large transverse slit, posterior, with or without lateral cuticular flaps. Postvulval uterine sac absent. Tail cylindroid, subcylindroid or tapering. **Male:** Cephalic region symmetrical or asymmetrical. Stylet rudimentary or absent. Oesophagus degenerate, often completely. Testis outstretched. Spicules small, slender, ventrally arcuate, cephalated, pointed. Gubernaculum small, fixed. Cloacal lips often raised, tubular. Bursa present (*Tylenchocriconema*, *Cacopaurus*) or absent (*Paratylenchus*). **Juveniles:** Most juveniles resemble female in stylet, oesophagus and body shape, occasionally later-stage juveniles may have degenerate oesophagus and no stylet. **Body curving upon relaxation.**

### Type subfamily

Paratylenchinae Thorne, 1949

### Other subfamily

Tylenchocriconematinae Raski & Siddiqui, 1975

### Key to subfamilies of Paratylenchidae

1. Female elongate-slender (L = about 0.5 mm or more; a = 40–70); male with asymmetrical head and a distinct bursa ..... **Tylenchocriconematinae**  
Female not elongate-slender (L under 0.5 mm; a < 35); male with symmetrical head and indistinct or no bursa ..... **Paratylenchinae**

## Subfamily Paratylenchinae Thorne, 1949

### Diagnosis

Paratylenchidae. **Body small (under 0.5 mm) and not extremely slender ( $a < 35$ ).** Male cephalic region symmetrical, stylet degenerate or absent. Female stylet well developed, with conus almost always much longer than the shaft. Vulva not overhung by anterior lip flap. Tail in female short, rounded, almost similar to that of male. Bursa lacking, side cuticle of tail may give an impression of a bursa (*Paratylenchus*), or if present then low, adanal (*Cacopaurus*).

### Type genus

*Paratylenchus* Micoletzky, 1922

#### Subgenera

*Paratylenchus* Micoletzky, 1922

*Gracilacus* Raski, 1962

### Other genus

*Cacopaurus* Thorne, 1943

### Note

*Paratylenchulus* De Grisse, 1972; *Paratylenchulus surinamensis* De Grisse, 1972; *Xenosphaeronema* De Grisse, 1972 and *Xenosphaeronema sphaerocephala* De Grisse, 1972 are nomina nuda.

### Key to genera of Paratylenchinae

1. Female obese-cylindroid; postvulval region shorter than vulval body width ..... *Cacopaurus*  
 Female vermiform, sometimes slightly obese but never cylindroid; postvulval region longer than vulval body width ..... *Paratylenchus*

### Genus *Paratylenchus* Micoletzky, 1922

syn. *Gracilacus* Raski, 1962

*Paratylenchoides* Raski, 1973

*Gracilpaurus* Ganguly & Khan, 1990

### Diagnosis

Paratylenchidae. Female under 0.5 mm, vermiform, or swollen in prevulval region; females and juveniles ventrally curved, often C-shaped on death. Annules fine or moderately coarse, round, smooth, not ornamented with tubercles. Lateral field with two, three or often four incisures. Cephalic region continuous, round, conoid or truncate, smooth or finely annulated, with or without four submedian lobes; framework with light to heavy sclerotization. **Female stylet 12–120  $\mu\text{m}$  long;** knobs spheroidal. Isthmus slender, basal bulb round to pyriform. **Excretory pore at level of nerve ring or more anterior, can be as far posterior as base of oesophagus.** Ovary outstretched. Postvulval uterine sac absent. Lateral vulval membranes present or absent. Male with stylet degenerate or absent. Oesophagus degenerate. Bursa absent. Spicules and gubernaculum usually 15–23  $\mu\text{m}$  and 3–5  $\mu\text{m}$  long, respectively.

## Type subgenus

*Paratylenchus* Micoletzky, 1922

## Other subgenus

*Gracilacus* Raski, 1962

Key to subgenera of *Paratylenchus*

1. Stylet 43–119  $\mu\text{m}$  long, excretory pore usually opposite median bulb or more anterior, mature females with a tendency to swell in prevulva region ..... *Gracilacus*
- Stylet under 40  $\mu\text{m}$  long, excretory pore usually near base of isthmus or opposite basal bulb, mature females not swelling abnormally ..... *Paratylenchus*

Subgenus *Paratylenchus* Micoletzky, 1922 (Siddiqi, 1986)

syn. *Paratylenchoides* Raski, 1973

(Fig. 135)

## Diagnosis

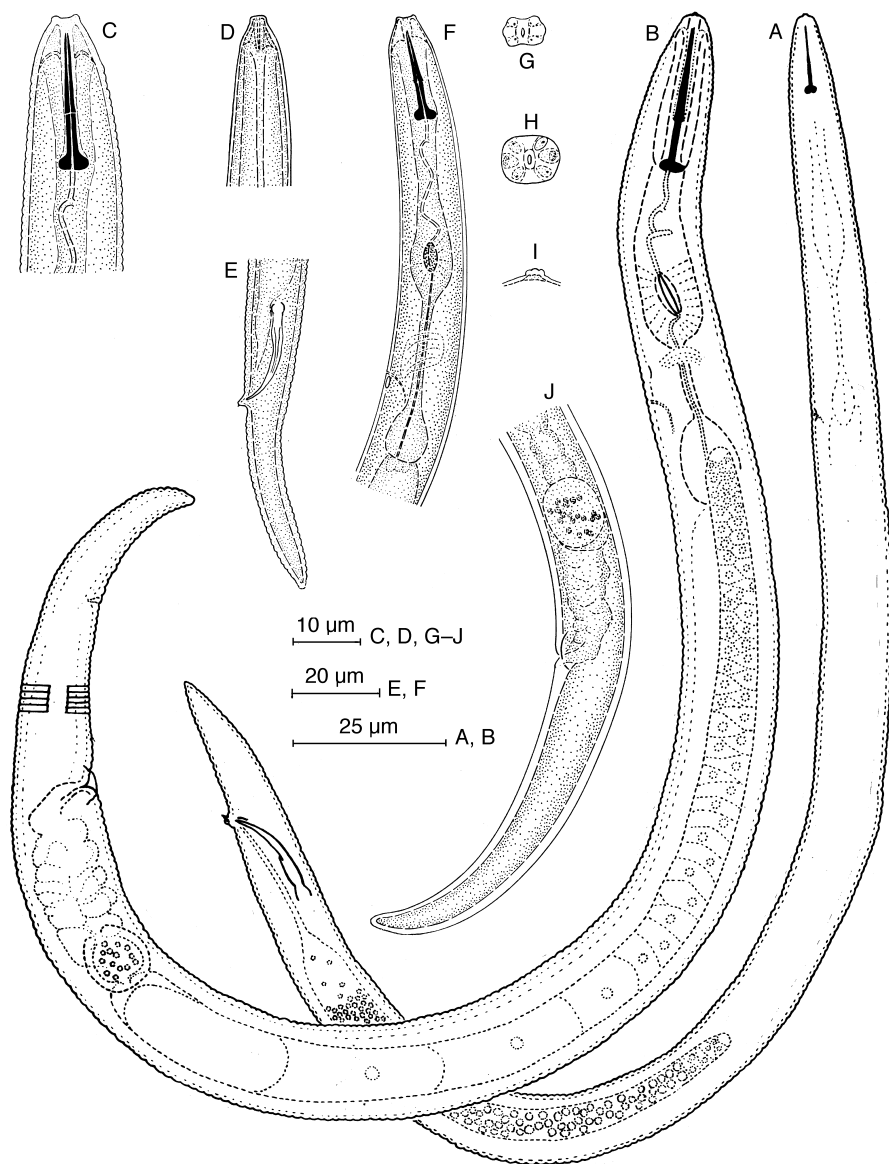
Genus *Paratylenchus*. Female vermiform, **not swelling abnormally**. Excretory pore usually near base of isthmus or opposite basal oesophageal bulb. Stylet 12–40  $\mu\text{m}$  long. Some juveniles with weak or no stylet.

## Type species

*Paratylenchus* (*Paratylenchus*) *bukowinensis* Micoletzky, 1922

## Other species

- Paratylenchus* (*Paratylenchus*) *acti* Eroshenko, 1978  
 syn. *Paratylenchus* (*Gracilacus*) *acti* Eroshenko, 1978  
*Gracilacus acti* (Eroshenko, 1978) Siddiqi, 1986
- P.* (*P.*) *alleni* Raski, 1975
- P.* (*P.*) *amblycephalus* Reuver, 1959 (syn. of *P. projectus* for Brzeski, 1998)
- P.* (*P.*) *amundseni* Bernard, 1982
- P.* (*P.*) *aquaticus* Merny, 1966  
 syn. *Paratylenchus humilis* Raski, 1975
- P.* (*P.*) *arculatus* Luc & de Guiran, 1962
- P.* (*P.*) *baldaccii* Raski, 1975
- P.* (*P.*) *besoekianus* Bally & Reydon, 1931 (sp. inq. for Brzeski, 1998)
- P.* (*P.*) *breviculus* Raski, 1975
- P.* (*P.*) *ciccaronei* Raski, 1975
- P.* (*P.*) *colbrani* Raski, 1975
- P.* (*P.*) *concavus* Eroshenko, 1978
- P.* (*P.*) *coronatus* Colbran, 1965
- P.* (*P.*) *curvatus* Van der Linde, 1938
- P.* (*P.*) *dianthus* Jenkins & Taylor, 1956
- P.* (*P.*) *discocephalus* Siddiqi, Khan & Ganguly, 1990
- P.* (*P.*) *duncani* Siddiqi, Baujard & Mounport, 1993
- P.* (*P.*) *elachistus* Steiner, 1949



**Fig. 135.** A and B. *Paratylenchus (Paratylenchus) bukowinensis* Micoletzky, male and female, respectively. C–J. *Paratylenchus (Paratylenchus) sheri* (Raski). C. Head end of female. D. Head end of male. E. Tail end of male. F. Oesophagus of female. G. *En face* view. H. Cross-section of head. I. Cross-section of body showing lateral ridge. J. Posterior region of female. (A and B. After Brzeski (1976): *CIH Descriptions of Plant-parasitic Nematodes*. C–J. After Raski (1973), courtesy Helminthological Society of Washington.)

- P. (P.) emarginatus* Eroshenko, 1978  
*P. (P.) emmoti* Dolinski, Souza & Huang, 1996  
*P. (P.) epicotylus* Siddiqi, Khan & Ganguly, 1990  
*P. (P.) flectospiculus* Huang & Raski, 1987  
*P. (P.) fueguensis* Raski & Valenzuela, 1986  
*P. (P.) goldeni* Raski, 1975  
*P. (P.) halophilus* Wouts, 1966  
*P. (P.) hamatus* Thorne & Allen, 1950  
*P. (P.) holdemani* Raski, 1975  
*P. (P.) israelensis* (Raski, 1973) Siddiqi, 1986 (a junior syn. of *P. sheri* for Talavera & Jiménez, 1997)  
     syn. *Paratylenchoides israelensis* Raski, 1973  
*P. (P.) italiensis* Raski, 1975 (syn. of *P. similis* for Brzeski, 1995)  
*P. (P.) juglansi* Kaul & Waliullah, 1990  
     syn. *Gracilacus juglansi* (Kaul & Waliullah) Esser, 1992  
*P. (P.) labiosus* Anderson & Kimpinski, 1977 (syn. of *P. similis* for Brzeski, 1995)  
*P. (P.) leiodermis* Raski, 1975  
*P. (P.) lepidus* Raski, 1975  
*P. (P.) leptos* Raski, 1975  
*P. (P.) longicaudatus* Raski, 1975  
*P. (P.) mexicanus* Raski, 1975  
*P. (P.) microdorus* Andrásy, 1959  
     syn. *P. brevihastus* Wu, 1962  
*P. (P.) mimulus* Raski, 1975 (syn. of *P. salubris* for Brzeski, 1998)  
*P. (P.) minor* Sharma, Sharma & Khan, 1987  
*P. (P.) minusculus* Tarjan, 1960  
*P. (P.) minutus* Linford, in Linford, Oliveira & Ishii, 1949  
*P. (P.) morius* Yokoo, 1970  
*P. (P.) musae* (Shahina & Maqbool, 1993) Brzeski, 1998  
     syn. *Gracilacus musae* Shahina & Maqbool, 1993  
*P. (P.) nainianus* Edward & Misra, 1963 (syn. of *P. arcuatus* for Brzeski, 1998)  
*P. (P.) nanus* Cobb, 1923  
*P. (P.) nawadus* Khan, Prasad & Mathur, 1967  
*P. (P.) neoamblycephalus* Geraert, 1965  
*P. (P.) neonanus* Mathur, Khan & Prasad, 1967  
*P. (P.) neoprojectus* Wu & Hawn, 1975  
*P. (P.) obtusicaudatus* Raski, 1975  
*P. (P.) pandus* Pinochet & Raski, 1977  
*P. (P.) paramonovi* Bagaturia & Solovyova in Solovyova, 1972  
*P. (P.) perlatus* Raski, 1975  
*P. (P.) perminimus* Siddiqi, 1996  
*P. (P.) pernoxius* Siddiqi, Baujard & Mounport, 1993  
*P. (P.) pesticus* Thorne & Malek, 1968  
*P. (P.) platyurus* Eroshenko, 1978  
*P. (P.) projectus* Jenkins, 1956  
*P. (P.) prunii* Sharma, Sharma & Khan, 1987  
*P. (P.) pseuduncinatus* Phukan & Sanwal, 1979

- P. (P.) recisus* Siddiqi, 1996  
*P. (P.) rostrocaudatus* Huang & Raski, 1987  
*P. (P.) rotundicephalus* Bajaj, 1988  
*P. (P.) salubris* Raski, 1975  
*P. (P.) serricaudatus* Raski, 1975  
*P. (P.) sheri* (Raski, 1973) Siddiqi, 1986  
     syn. *Paratylenchoides sheri* Raski, 1973  
*P. (P.) similis* Khan, Prasad & Mathur, 1967  
*P. (P.) tateae* Wu & Townshend, 1973 (syn. of *P. similis* for Brzeski, 1995)  
*P. (P.) tenuicaudatus* Wu, 1961  
*P. (P.) triincisus* Bajaj, 1988  
*P. (P.) tui* Orton Williams, 1985  
*P. (P.) uncinatus* Samibaeva, 1966  
*P. (P.) vandenbrandei* De Grisse, 1962  
*P. (P.) variabilis* Raski, 1975  
*P. (P.) variatus* Jairajpuri, 1982  
*P. (P.) veruculatus* Wu, 1962  
*P. (P.) vexans* Thorne & Malek, 1968

#### Species inquirendae

- Paratylenchus macrophallus* (de Man, 1880) Goodey, 1934  
     syn. *Tylenchus macrophallus* de Man, 1880  
     *Anguillulina macrophallus* (de Man) Goodey, 1932  
*Paratylenchus strenzkei* (Volz, 1951) Oostenbrink, 1960  
     syn. *Hemicycliophora* (= *Procriconema*) *strenzkei* Volz, 1951

#### Nomina nuda

- Paratylenchus nanus* var. *bicaudatus* Gubina, 1973  
*Paratylenchus esculentus* Brown, 1959 (appears in Siddiqi (1986) and Raski & Luc (1987)  
*Gracilacus esculentus* (Brown, 1959) Raski, 1962; (appears in Siddiqi (1986) and Raski & Luc (1987)

ETYMOLOGY. From Greek *para* = beside or near, and *Tylenchus*.

The type species was found in sandy meadow soil near River Prut, close to Czernovitz, Ukraine. A detailed key to *Paratylenchus* spp. is given by Esser (1992).

#### Subgenus *Gracilacus* Raski, 1962 (Siddiqi, 1986)

syn. *Gracilpaurus* Ganguly & Khan, 1990

(Fig. 136, M–Q)

#### Diagnosis

Genus *Paratylenchus*. Immature female vermiform with ovary having only a few oocytes; **mature female swollen in prevulva region and with well-developed ovary**, 0.24–0.44 mm long. **Cuticle rarely ornamented with warts and tubercles**. Cephalic region rounded or discoidal with large submedian lobes in some species



(*P. (G.) capitatus*, *P. (G.) longilabiatus*). Female stylet 41–119  $\mu\text{m}$  long, flexible. Excretory pore generally in region of postcorpus but variable from near stylet knobs to opposite nerve ring. Vulva at 67–84% of body length, with or without lateral membranes. Spicules 15–24  $\mu\text{m}$  long. Third-stage juveniles may lack stylet but other juveniles with well-developed stylet.

#### Type species

*Gracilacus epacris* (Allen & Jensen, 1950) Raski, 1962

#### Present status

*Paratylenchus (Gracilacus) epacris* (Allen & Jensen, 1950) Goodey, 1963

syn. *Cacopaurus epacris* Allen & Jensen, 1950

*Gracilacus epacris* (Allen & Jensen) Raski, 1962

*Paratylenchus epacris* (Allen & Jensen) Goodey, 1963

#### Other species

*Paratylenchus (Gracilacus) abietis* Eroshenko, 1974

syn. *Paratylenchus abietis* Eroshenko, 1974 (syn. of *P. straeleni* for Brzeski, 1998)

*Gracilacus abietis* (Eroshenko) Raski, 1976

*P. (G.) aciculus* Brown, 1959

syn. *Paratylenchus aciculus* Brown, 1959

*Gracilacus acicula* (Brown) Raski, 1962

*P. (G.) aculentus* Brown, 1959

syn. *Paratylenchus aculentus* Brown, 1959

*Gracilacus aculenta* (Brown) Raski, 1962

*P. (G.) anceps* Cobb, 1923

syn. *Paratylenchus anceps* Cobb, 1923

*Gracilacus anceps* (Cobb) Raski, 1962

*P. (G.) aonli* Misra & Edward, 1971

syn. *Paratylenchus aonli* Misra & Edward, 1971

*Gracilacus aonli* (Misra & Edward) Raski, 1976

*P. (G.) bilineatus* (Brzeski, 1995) Brzeski, 1998

syn. *Gracilacus bilineata* Brzeski, 1995

*P. (G.) brasiliensis* (Huang & Raski, 1986) Brzeski, 1998

syn. *Gracilacus brasiliensis* Huang & Raski, 1986

*P. (G.) capitatus* (Adams & Eichenmuller, 1962) Siddiqi & Goodey, 1964

syn. *Gracilacus capitata* Adams & Eichenmuller, 1962

*Paratylenchus capitatus* (Adams & Eichenmuller) Siddiqi & Goodey, 1964

(syn. of *P. marylandicus* for Brzeski, 1998)

*P. (G.) colinus* (Huang & Raski, 1986) Brzeski, 1998

syn. *Gracilacus colina* Huang & Raski, 1986

*Gracilpaurus colinus* (Huang & Raski) Ganguly & Khan, 1990

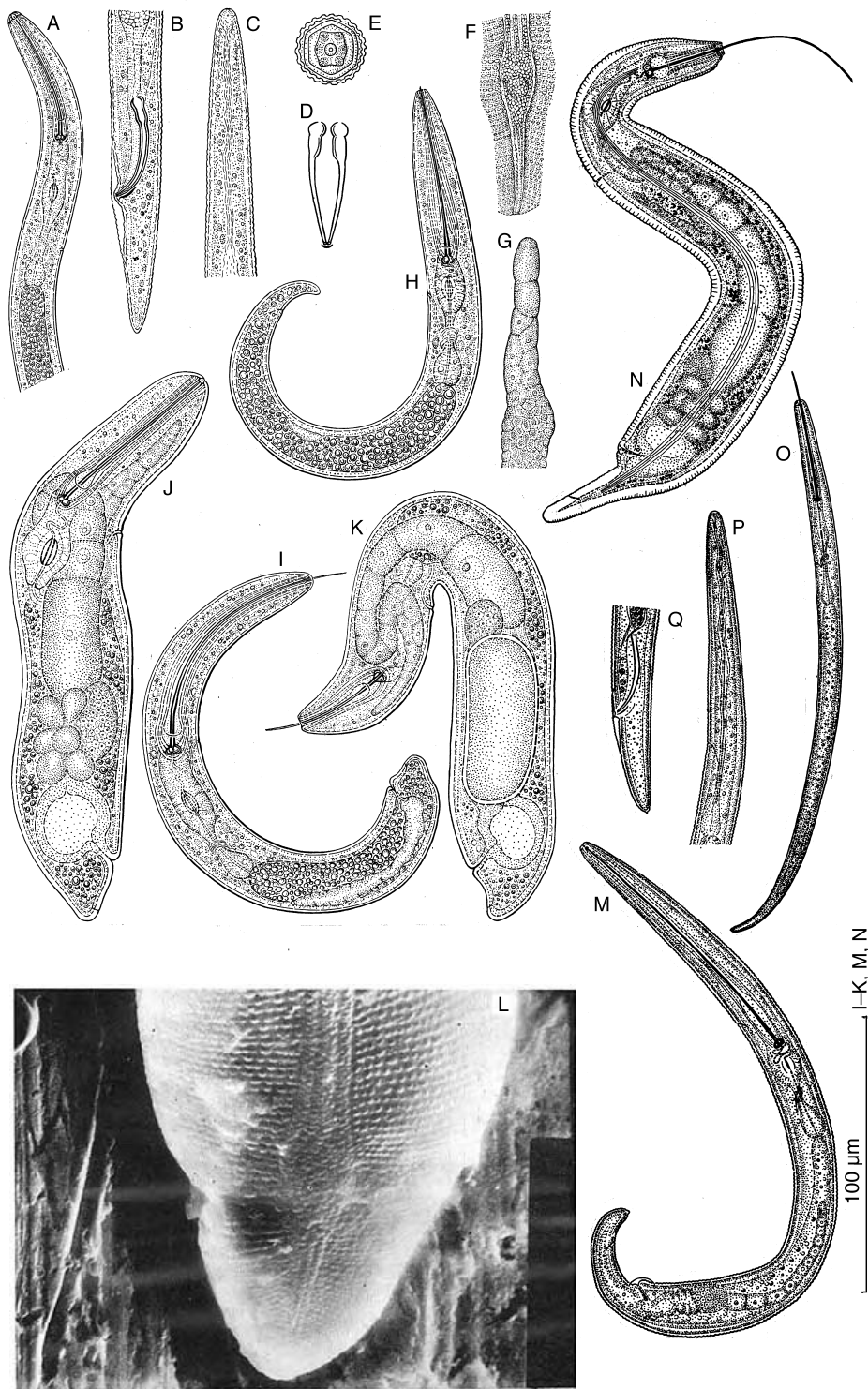
*P. (G.) corbetti* (Ganguly & Khan, 1990) comb. n.

syn. *Gracilpaurus corbetti* Ganguly & Khan, 1990

*Gracilacus corbetti* (Ganguly & Khan) comb. n.

*P. (G.) costatus* (Raski, 1976) Siddiqi, 1986

syn. *Gracilacus costata* Raski, 1976



- P. (G.) crenatus* Corbett, 1966  
 syn. *Paratylenchus crenatus* Corbett, 1966  
*Gracilacus crenata* (Corbett) Raski, 1976  
*Gracilacus crenata* (Corbett) Nesterov, 1979  
*Gracilpaurus crenatus* (Corbett) Ganguly & Khan, 1990
- P. (G.) elegans* (Raski, 1962) Siddiqi & Goodey, 1964  
 syn. *Gracilacus elegans* Raski, 1962
- P. (G.) elongatus* (Abdel-Rahman & Maggenti, 1988) Brzeski, 1998  
 syn. *Gracilacus elongata* Abdel-Rahman & Maggenti, 1988
- P. (G.) enatus* (Raski, 1976) Siddiqi, 1986  
 syn. *Gracilacus enata* Raski, 1976
- P. (G.) goodeyi* Oostenbrink, 1953  
 syn. *Paratylenchus goodeyi* Oostenbrink, 1953  
*Gracilacus goodeyi* (Oostenbrink) Raski, 1962
- P. (G.) hamicaudata* (Cid del Prado Vera & Maggenti, 1988) Brzeski, 1998  
 syn. *Gracilacus hamicaudata* Cid del Prado Vera & Maggenti, 1988
- P. (G.) idalimus* (Raski, 1962) Siddiqi & Goodey, 1964  
 syn. *Gracilacus idalimus* Raski, 1962  
*Paratylenchus idalimus* (Raski) Siddiqi & Goodey, 1964
- P. (G.) intermedius* (Raski, 1962) Siddiqi & Goodey, 1964  
 syn. *Gracilacus intermedia* Raski, 1962  
*Paratylenchus intermedius* (Raski) Siddiqi & Goodey, 1964
- P. (G.) ivorensis* Luc & de Guiran, 1962  
 syn. *Paratylenchus ivorensis* Luc & de Guiran, 1962  
*Gracilacus ivorensis* (Luc & de Guiran) Raski, 1976
- P. (G.) janai* (Baqri, 1979) Siddiqi, 1986  
 syn. *Gracilacus janai* Baqri, 1979  
*Paratylenchus janai* (Baqri) Siddiqi, 1986
- P. (G.) latescens* (Raski, 1976) Siddiqi, 1986  
 syn. *Gracilacus latescens* Raski, 1976  
*Paratylenchus latescens* (Raski) Siddiqi, 1986
- P. (G.) longilabiatus* (Huang & Raski, 1986) Brzeski, 1998  
 syn. *Gracilacus longilabiata* Huang & Raski, 1986
- P. (G.) macrodorus* Brzeski, 1963  
 syn. *Paratylenchus macrodorus* Brzeski, 1963  
*Gracilacus macrodorus* (Brzeski) Raski, 1976  
*Paratylenchus longistylus* Dement'eva, 1972  
*Gracilacus longistylusa* (Dement'eva) Nesterov, 1979

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**Fig. 136. opposite** A–L. *Cacopaurus pestis* Thorne. M–Q. *Paratylenchus* (*Gracilacus*) *epacris* Allen & Jensen. A. Oesophagus of juvenile. B and Q. Tail ends of males. C and P. Head ends of males. D. Spicules. E. *En face* view of female. F and L. Cuticular pattern and lateral field in posterior regions of females, respectively. G. Tip of testis. H. Female juvenile. I and M. Young females. J, K and N. Mature females. O. Young juvenile. (A–K. After Thorne (1943). M–Q. After Allen & Jensen (1950), courtesy Helminthological Society of Washington. L. After Bello & Belart (1975), courtesy *Nematologica Mediterranea*.)

- P. (G.) marylandicus* Jenkins, 1960  
 syn. *Paratylenchus marylandicus* Jenkins, 1960  
*Gracilacus marylandica* (Jenkins) Raski, 1962 (syn. of *G. capitatus* for Geraert, 1965)
- P. (G.) micoletzkyi* Edward, Misra & Singh, 1967  
 syn. *Paratylenchus micoletzkyi* Edward, Misra & Singh, 1967  
*Gracilacus micoletzkyi* (Edward, Misra & Singh) Raski, 1976
- P. (G.) mirus* (Raski, 1962) Siddiqi & Goodey, 1964  
 syn. *Gracilacus mira* Raski, 1962  
*Paratylenchus mirus* (Raski) Siddiqi & Goodey, 1964
- P. (G.) mutabilis* Colbran, 1969  
 syn. *Paratylenchus mutabilis* Colbran, 1969  
*Gracilacus mutabilis* (Colbran, 1969) Raski, 1976  
*Gracilpaurus mutabilis* (Colbran) Ganguly & Khan, 1990  
*Gracilacus punctata* Huang & Raski, 1986 (syn. by Ganguly & Khan, 1990)  
*Gracilpaurus punctatus* (Huang & Raski) Ganguly & Khan, 1990  
*Paratylenchus punctatus* (Huang & Raski) Geraert, 1998
- P. (G.) oostenbrinki* Misra & Edward, 1971  
 syn. *Paratylenchus oostenbrinki* Misra & Edward, 1971  
*Gracilacus oostenbrinki* (Misra & Edward, 1971) Raski, 1976
- P. (G.) oryzae* (Sharma, Edward, Misra & Chandrashekar, 1992) comb. n.  
 syn. *Gracilacus oryzae* Sharma, Edward, Misra & Chandrashekar, 1992
- P. (G.) pandatus* (Raski, 1976) Siddiqi, 1986  
 syn. *Gracilacus pandata* Raski, 1976  
*Paratylenchus pandatus* (Raski) Siddiqi, 1986
- P. (G.) parvulus* (Raski, 1976) Siddiqi, 1986  
 syn. *Gracilacus parvula* Raski, 1976  
*Paratylenchus parvulus* (Raski) Siddiqi, 1986
- P. (G.) peperpotti* (Schoemaker, 1963) Siddiqi & Goodey, 1964  
 syn. *Gracilacus peperpotti* Schoemaker, 1963  
*Paratylenchus peperpotti* (Schoemaker) Siddiqi & Goodey, 1964
- P. (G.) peraticus* (Raski, 1962) Siddiqi & Goodey, 1964  
 syn. *Gracilacus peratica* Raski, 1962  
*Paratylenchus peraticus* (Raski) Siddiqi & Goodey, 1964
- P. (G.) raskii* (Phukan & Sanwal, 1979) Siddiqi, 1986  
 syn. *Gracilacus raskii* Phukan & Sanwal, 1979  
*Paratylenchus raskii* (Phukan & Sanwal) Siddiqi, 1986
- P. (G.) robustus* Wu, 1974  
 syn. *Paratylenchus robustus* Wu, 1974  
*Gracilacus robusta* (Wu) Raski, 1976
- P. (G.) solivagus* (Raski, 1976) Siddiqi, 1986  
 syn. *Gracilacus solivaga* Raski, 1976  
*Paratylenchus solivagus* (Raski) Siddiqi, 1986
- P. (G.) steineri* Golden, 1961  
 syn. *Paratylenchus steineri* Golden, 1961  
*Gracilacus steineri* (Golden) Raski, 1962
- P. (G.) straeleni* (de Coninck, 1931) Oostenbrink, 1960

- syn. *Procriconema straeleni* de Coninck, 1931  
*Hemicycliophora straeleni* (de Coninck) Loos, 1948  
*Paratylenchus straeleni* (de Coninck) Oostenbrink, 1960  
*Gracilacus straeleni* (de Coninck, 1931) Raski, 1976  
*Paratylenchus audriellae* Brown, 1959 (original spelling *audriella*)  
*Gracilacus audriellae* (Brown) Raski, 1962  
*Paratylenchus sarissa* Tarjan, 1960  
*Gracilacus sarissa* (Tarjan) Raski, 1962  
*P. (G.) teres* (Raski, 1976) Siddiqi, 1986  
 syn. *Gracilacus teres* Raski, 1976  
*Paratylenchus teres* (Raski) Siddiqi, 1986  
*P. (G.) verus* (Brzeski, 1995) Brzeski, 1998  
 syn. *Gracilacus vera* Brzeski, 1995  
*P. (G.) yokooi* (Toida, Ohshima & Hirata, 1983) Brzeski, 1998  
 syn. *Gracilacus yokooi* Toida, Ohshima & Hirata, 1983

ETYMOLOGY. From Latin *gracilis* = slender, and *acus* = pin, needle (for stylet). The name is feminine in gender due to *acus* being so.

The type species was found parasitizing roots of Californian black walnut, *Juglans hindsii* Jepson in Visalia, Tulare County, California, USA. A detailed key to *Gracilacus* spp. is given by Esser (1992).

### Genus *Cacopaurus* Thorne, 1943

(Fig. 136, A–L)

#### Diagnosis

Paratylenchinae. Very small-sized (0.2–0.3 mm), mature female obese. **Female:** **Cylindroid-obese**, five to eight times as long as wide. Young females ventrally arcuate, older females straight or bent behind oesophagus. Cuticle thin, **annules** 1  $\mu\text{m}$  wide at midbody, **ornamented with minute tubercles**. Lateral field with four incisures ornamented with rows of tubercles. Cephalic region smooth, framework obscure. **Stylet 92–102  $\mu\text{m}$  or about one-third as long as body**; conus about six times as long as shaft; knobs minutely rounded. Oesophagus typical of the family. Vulva near posterior end, cleft-like; **postvulval region of body conoid-rounded, shorter than vulva body width**. Uterus forming a thick-walled chamber; no postvulval sac; ovary with double flexures. Anus obscure. **Male:** Annules coarse, unornamented. Lateral field with three or four faint incisures. Deirid reported opposite anterior end of intestine. Oesophagus degenerate; stylet absent. Spicules slender, arcuate, cephalated. Gubernaculum thin. Tail short (about three anal body widths), slightly tapering to a round terminus. **Bursa small, adanal. Juveniles:** Vermiform with **well-developed stylet**. Cephalic region continuous, smooth; framework lightly sclerotized. Excretory pore opposite isthmus. Tail elongate-conoid with bluntly rounded tip. Adult female **sedentary** root ectoparasite.

### Type species

*Cacopaurus pestis* Thorne, 1943

syn. *Paratylenchus pestis* (Thorne) Goodey, 1963

No other species.

ETYMOLOGY. Derived from Greek *kakos* = bad, and *pauros* = small (a bad small nematode).

The type species parasitizes roots of *Juglans regia*, the Persian walnut, var. Mayette, at Santa Clara, California, USA.

## Subfamily Tylenchocriconematae Raski & Siddiqui, 1975

### Diagnosis

Paratylenchidae. **Medium-sized nematodes with slender body** (0.42–0.83 mm; a = 40–70); both sexes vermiform. Marked sexual dimorphism in anterior region. Female normal, **male with an asymmetrical, ventrally inclined cephalic region**, degenerated oesophagus and no stylet. Stylet of female short but with cone longer than shaft. Vulva overhung by anterior lip flap. **Female tail long and slender, tip pointed**. Male tail also long, tapering, **completely enveloped by a distinct bursa**.

### Type genus

*Tylenchocriconema* Raski & Siddiqui, 1975

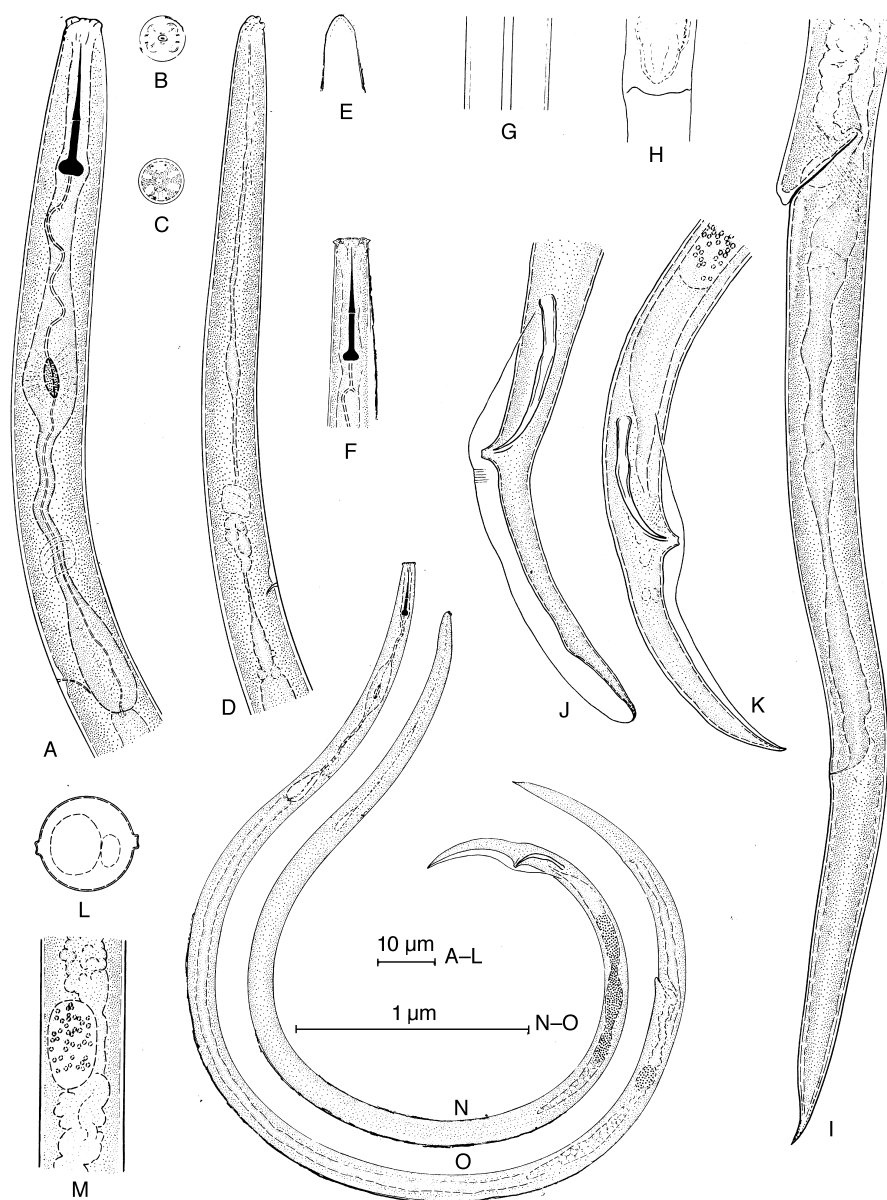
No other genus.

## Genus *Tylenchocriconema* Raski & Siddiqui, 1975

(Fig. 137)

### Diagnosis

Tylenchocriconematae. With characters of the family. Lateral field slightly raised, with four incisures; three ridges seen in SEM. **Female:** Cephalic region very low, truncate, with squarish oral plate, an I-shaped oral aperture flanked by two lateral liplets and four small submedian lobes or pseudolips at corners of oral plate; amphidial apertures in the form of dorso-ventral slits at base of lateral liplets (see SEMs in Raski & Luc, 1987); framework weak, vestibulum extension appearing as slender dark rods. Stylet of female about 20–30 µm long, knobs rounded. Orifice of dorsal gland 5–6 µm behind stylet base. Excretory pore near basal bulb. Deirids absent. **Vulva slightly overhung by anterior lip flap and with small lateral membranes**, well marked by a sudden narrowing of body contour behind it, at 78–81% of body length. Vagina, cuticularized, directed inward and forward. Postvulval uterine sac absent. Spermatheca thin-walled, oval, offset, with minute, round sperm. Female tail straight, elongate (over five anal body widths long), subcylindroid to conoid-pointed tip. **Male:** 0.42–0.65 mm long, shorter and more slender than female. Lateral field with four incisures. Head end asymmetrical, with ventrally directed cephalic region bearing four submedian lobes; framework indistinct. Oesophagus degenerate, stylet absent. Testis outstretched. Cloacal lips forming a penial tube. Tail elongate-conoid, arcuate ventrally; **bursa enclosing tail tip**, with crenate margins.



**Fig. 137.** *Tylenchocriconema alleni* Raski & Siddiqui. D, E, J, K and N. Males. F. Juvenile. Remainder females. A and D. Oesophageal regions. B and C. *En face* view and cross-section of head, respectively. E and F. Anterior ends. G and L. Lateral fields. H. Vulva in ventral view. I-K. Tail ends. M. Spermatheca. N and O. Entire adults. (After Raski & Siddiqui (1975), courtesy *Journal of Nematology*.)

Spicules arcuate, cephalated, pointed. Gubernaculum small, fixed. Juveniles similar to female in body shape, cephalic region, stylet and oesophagus; tail evenly tapering to an acute tip.

#### Type species

*Tylenchocriconema alleni* Raski & Siddiqui, 1975

No other species.

ETYMOLOGY. From prefix of Tylenchoidea, and of Criconematoidea (the authors believed the superfamily Tylenchocriconematoidea to be intermediate between those superfamilies).

The type species was found in soil around roots of an unidentified bromeliad shipped to the USA from Guatemala. It occurs in large numbers in the crowns of the bromeliad the *Tillandsia flabellata* Bak. and feeds on leaf surfaces and in the crown tissues.



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# IX Suborder Hexatyline

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## SUBORDER HEXATYLINA SIDDIQI, 1980

syn. *Sphaerulariina* Maggenti, 1982

*Allantonematina* Inglis, 1983

*Heterotylenchina* Inglis, 1983

### Diagnosis

Tylenchida. **Primarily entomoparasitic, mostly with free-living mycetophagous or plant-parasitic** (e.g. *Fergusobia*) generation. Female of several genera di-, tri- or tetramorphic according to feeding habits. **Entomoparasitic generation with only adult female parasitic in insect or mite haemocoel**, other stages in host non-parasitic; obese adults occurring in arthropod haemocoel and in plant galls (*Fergusobia*). Obese haemocoel-inhabiting female usually with microvilli on body surface and canal-like formation in body-wall indicating **absorption of food from general body surface**; a cuticle in such forms may be lacking. Cuticle smooth or finely annulated. Lateral fields present or absent. Deirids usually present. **Phasmids and prophasms not known**. Cephalic region generally low, smooth or finely striated; supporting framework six-, eight-, or 12-sectored, with little or no sclerotization; **no labial disc or submedian lobes**; **amphidial apertures dorso-sublateral**, pore- or oblique slit-like, at about the level of four cephalic sensilla which are on surface; six inner labial sensilla around minute pore-like oral opening. Stylet generally under 20 µm long (hypertrophied in preadult insect-parasitic female), with or without basal knobs. Orifice of dorsal gland close to or at some distance behind stylet. Oesophagus in entomoparasitic forms not divisible into corpus, isthmus and basal region. Oesophageal glands three, but only two reported for *Sphaerularia* and *Tripilus*, contained in a basal bulb or extending over intestine. **Nerve ring circum-intestinal in insect-parasitic forms**, circum-oesophageal in free-living stage. Excretory duct not vesiculate terminally. **A cellular cardia absent**. Intestine oligocytous, may be

syncytial. Rectum may act as a feeding pump (e.g. *Hexatylys*) in free-living stage. Anus pore-like, atrophied in saccate females. Tails of juveniles and adults over one anal body width long. **Female: Monodelphic, prodelphic.** Free-living female with a short slender stylet, oesophagus with corpus, isthmus and basal region and nerve ring encircling isthmus or subcylindroid with oesophago-intestinal valve anterior to nerve ring. Preadult entomoparasitic female with hypertrophied stylet (= pseudostylet) and oesophagus, small vulva, elongated uterus serving as storage for sperm, in adult female often with several eggs and/or juveniles, sometimes everted and hypertrophied to lead an independent life (= uterium of *Sphaerularia* and *Prothallonema*). **Crustaformeria** in the form of a **quadricolumella or with more than four rows of cells, never a tricolumella.** Oviduct with two consecutive rings of four cells each (*Hexatylys*) or with two rows of more than three cells each. Ovary single, outstretched, reflexed at tip or coiled; **a rachis may be present** in forms inhabiting insect haemocoel. Vagina may be tuboid and strongly muscular and uterus may prolapse in some insect-parasitic forms. Vulva a large transverse slit, oval, or small pore-like, located posteriorly usually at over 85% of body length. **Male:** With or rarely without a stylet. Oesophagus as in free-living female, or rarely degenerated. Testis single, outstretched or with tip reflexed, with or without a rachis, functional or degenerate in adult, spermatogenesis in the latter case probably occurring before the final moult (cf. Criconematina). Several thousand round or amoeboid sperm produced by forms of entomoparasitic generation, much less by plant-parasitic or mycetophagous forms. Spicules small (usually under 30 µm long), paired, arcuate, cephalated or in Iotonchiidae **large, robust and angular;** never setaceous. **Gubernaculum simple, fixed, may be lacking.** Bursa simple, neither lobed nor with phasmidial pseudoribs, may be absent. Hypoptygma single; caudal papillae absent except for *Fungiotonchium*, which has a midventral papilla (? = hypoptygma) a little behind cloacal aperture.

#### Type genus

*Hexatylys* Goodey, 1926

#### Type superfamily

Neotylenchoidea Thorne, 1941

#### Present status

Sphaerularioidea Lubbock, 1861  
syn. Neotylenchoidea Thorne, 1941

#### Other superfamily

Iotonchioidea Goodey, 1953

#### Relationship and discussion

For relationship with Tylenchina see under that suborder. Hexatylinea differs from the Criconematina in the structure of the cephalic region and oesophagus of the juveniles and females, in the male spicules not being setaceous, semicircular or U-shaped, and in their habit of mycetophagy and insect parasitism.

Siddiqi (1980) proposed the suborder Hexatylinea which together with

Tylenchina, Criconematina and Myenchina, constituted the order Tylenchida. In Hexatyline, Siddiqi included the superfamilies Neotylenchoidea, Allantonematoidea and Sphaerularioidea, which show a gradual evolution from fungus-feeding to parasitizing insects, even in the same genus. Later, Siddiqi (1986) recognized under Hexatyline four superfamilies, viz. Neotylenchoidea, Anguinoidea, Iotonchioidea and Sphaerularioidea. However, unlike other superfamilies, Anguinoidea lack an insect-parasitic phase in their life history and represent 'a unique line among the Tylenchida that evolved from fungal-feeding forms, the line culminating in highly specialized stem and seed parasites' (Siddiqi, 1983a). This superfamily is here assigned to a new infraorder Anguinata of the suborder Tylenchina. Neotylenchoidea is proposed as a synonym of Sphaerularioidea since the insect-parasitic genera *Hexatylus* and *Deladenus* are known to have an insect-parasitic phase in their life cycles and thus are similar to *Prothallonema* of the Sphaerulariidae. Hexatyline now has two superfamilies – Sphaerularioidea and Iotonchioidea.

Maggenti (1982) proposed the suborder Sphaerulariina for the Sphaerularioidea which are exclusively insect-parasitic. Inglis (1983) established two new orders, Allantonematida and Myenchida, as well as two new suborders, Allantonematina and Heterotylenchina. Inglis's (1983) action was based on his 'combined assessment of phylogenetic origins and of morphological diversity-difference'. However, it appears to be too ambitious since the allantonematids and heterotylenchids show neither different phylogenetic origins nor sufficient morphological diversity to justify separate suborders.

It should be noted that Iotonchiidae, with their huge, L-shaped spicules, large postanal papilla on the male tail, a midventral postvulval sensillum and a large anterior vulval lip flap, may indicate a different phylogenetic line. Iotonchiidae have two types of parasitic female in the insect host, but this feature is also shared by Parasytylenchidae, which in their morphology are quite similar to allantonematids which lack a secondary generation in the host. Both groups belong to Hexatyline.

All these nematodes constitute one whole that must have evolved a long time ago from a common ancestor, and represents the suborder Hexatyline. As pointed out by Siddiqi (1980), 'The alternation of free-living and parasitic generations and di-, tri- or tetramorphic females in Hexatyline clearly indicate that they have evolved from ancestors that were highly adapted to parasitism of lower plants and animals. Their primitive stylet, oesophagus and monodelphy show that they are a conservative group and that the Tylenchina and Criconematina probably evolved from ancestors resembling them.'

The ability of Hexatyline to pierce the body-wall of an insect host and thus gain direct access to the haemocoel is an extraordinary adaptation. It must be an ancient trait that laid the foundation of insect parasitism. In contrast to plant and animal parasites (e.g. *Heterodera*, *Ancylostoma*), the stage of the Hexatyline entering the host is a fertilized female, often still inside the fourth-stage juvenile cuticle. The female mates when its ovary is still under-developed (i.e. by korigamie, the term used by Wülker, 1923). This female carries an immense load of sperms, at times numbering several thousands, in an extensile uterus. This is an adaptation to parasitism of the insect haemocoel where the male cannot gain entry into the insect host along with the female since the male lacks a powerful boring stylet and a parasitic way of life.

The penetration of the host cuticle is an important achievement resulting from the slenderness of the female body and hypertrophy of the stylet and oesophageal glands. A typical example of host penetration was reported by Poinar & Doncaster (1965), who studied the penetration of *Tripus sciarae* into the host larva of *Bradysia paupera*. The female of *Tripus* that penetrates the insect larva is ensheathed in a second cuticle, probably that of the fourth-stage juvenile, and is impregnated through this second cuticle in free life. The impregnated female uses both stylet and enzymes from the oesophageal glands during the process of penetration. The glandular secretions act as exsheathing fluid and, with the outer cuticle, produce an adhesive mass which anchors the nematode to the host. The nematode then begins thrusting its stylet against the host's cuticle, at an average rate of two thrusts per second, with long slower thrusts between the short quicker ones. Only the stylet conus is thrust and the gland secretions are seen to move forward with the stylet action and they may also help chemically in the penetration process. Finally the nematode forces its way through the weakened and injured cuticular area. When about one-third of the body has penetrated, entry becomes easier and the female glides smoothly into its host. After the entry the adhesive mass seals the entrance hole, thereby avoiding the risk of microbial infections which might kill the host.

In Hexatylna, all the species have the adult heterosexual female as the primary parasite of the insect or mite haemocoel. Secondary parasitic females are found in some genera, as either heterosexual (*Parasitylenchus*) or parthenogenetic (*Heterotylenchus*) forms. The primary heterosexual female is well adapted to obtain nourishment from its general body surface. Its stylet and oesophagus become non-functional and the latter loses connection with the intestine. The rectum and anus degenerate, the intestine probably serving only as a storage organ. The body surface has microvilli to increase the absorption area, as found in *Howardula husseyi* and *Deladenus siricidicola* by Riding, 1970 and 1970a, respectively. Numerous irregularly-shaped canals, possibly concerned with food assimilation, have been found in the cuticle of the primary parasitic heterosexual female of a *Heterotylenchus* sp. (Nicholas, 1972). Subbotin *et al.* (1994) showed that entomoparasitic females of *Wachekitylenchus bembidi* and *Allantonema mirabile* lacked cuticle and in its place had a microvillous layer to help in food absorption. The alternative method of food absorption is through prolapsed hypertrophied uterine cells (*Tripus*) or the entire uterus (*Sphaerularia*).

Numerous interwoven cytoplasmic hypodermal processes in the form of microvilli cover the entire body of insect-parasitic females of *Skarbilovinema laumondi* Chizhov & Zakharenkova, 1991. The cuticle is completely reduced and the body-wall is composed mainly of the well-developed hypodermis. The microvilli form a 'spongy layer' which is considered to be a special adaptation to increase the absorptive surface for a more effective uptake of nutrients from the insect haemocoel. Subbotin *et al.* (1993) believe that the surface structure of the body cuticle can be used in the systematics of insect-parasitic tylenchids since *Howardula husseyi* lacks a cuticle and the hypodermal membrane that covers the body surface has numerous microvilli and *Paraitonchium nicholasi* has a well-developed cuticle with numerous ramified canals running from the hypodermis to the outer surface (Nicholas, 1972).

The primary heterosexual female is always fertilized in the external environment and, since it produces a large number of eggs in the insect or mite haemocoel,

receives an enormous amount of sperm during mating. However, with a large sperm load, the female remains slender as the sperm are stored in a very elongated uterus extending almost up to the middle of the body and the ovary remains under-developed. After penetrating the host, the female generally grows to a large sausage-shaped or spheroidal structure and as the egg production begins, the sperm accumulate in special large membranous pouches (= spermatheca) located in the uterus near its junction with the oviduct.

Since the time of Leuckart (1884), most nematologists and parasitologists working with insect nematodes believed that the parasitic female was protandric hermaphroditic until Wülker (1923) showed that it was in fact heterosexual and that it entered the host already having received sperm. Bovien (1944) demonstrated that the process of spermatogenesis was already completed in the preadult male in which the entire gonoduct was filled with sperm. This was noted by Wülker (1923) and Bovien (1944) for *Allantonema mirabile* and *Tripius sciarae*, respectively.

Bovien (1937) pointed out that, since the insect-parasitic Tylenchida did not have a free-living stage, the previously held idea that those nematodes were heterogonic had to be abandoned. But recently the concept has gained new currency, and I believe that several insect-parasitic tylenchid genera have as yet unrecognized free-living generations.

The recently described *Anandranema phlebotophagum* Poinar *et al.*, 1993 is the only known allantonematid that multiplies by autotoky (multiplication by a single parent). This species is hermaphroditic and sperm found in the hermaphrodites are small, being 1–2  $\mu\text{m}$  in diameter. The infective-stage hermaphrodite has an inconspicuous vulva and is small, only 277–365 (324)  $\mu\text{m}$  long. It penetrates directly through the body-wall of a first-stage sand fly (*Lutzomyia longipalpis*) larva and develops into an elongate cylindrical form that has a well-developed reproductive tract and that absorbs nutrients through the cuticle. Egg development begins in the larva and continues in the pupa and adult sand fly. Hermaphrodites are pleomorphic, assuming a variety of body shapes. Eggs are deposited into the host's haemocoel, where they hatch and juvenile development continues to late third stage. The juveniles accumulate in the sand fly, sometimes packing its body cavity, and exit via its anus or ovipositor (Poinar *et al.*, 1993).

The life cycles of Hexatylna can be grouped into three broad categories as follows:

**ALLANTONEMATOID LIFE CYCLE.** As summarized by Bovien (1944), the life cycle of typical Allantonematidae involves the spermatized, slender female penetrating the insect or mite host and developing in the haemocoel where it undergoes a more or less radical transformation. The parasitic female attains full maturity in the adult host. Upon entering a host's larva, pupa or nymph, its development is generally synchronized with that of the host. It increases in size and the genital organs gradually fill most of the body cavity. The eggs and, in the case of ovoviviparous species, the juveniles are set free in the host's haemocoel. The eggs hatch and the juveniles moult and develop to the third or fourth stage and search for an exit. They may escape through the genital aperture by reaching the ovary and oviduct, by penetrating the gut wall and escaping through the anus, or occasionally by penetrating the body-wall. In the free life, the male undergoes a final moult and mates with the

female which is usually still within the juvenile's cuticle. The male then dies and the female invades a new host. Thus in a single heterosexual cycle, both parasitic and free-living forms are found, although the latter are usually only partially free-living, as they do not feed or multiply in the soil. Sometimes the mating individuals do not reach the soil, e.g. *Howardula aptini* mates inside the plant galls produced by its host thrips and there it infects the host larva or pupa and *H. apioni*, a parasite of the weevil, *Apion carduorum*, has its free stage in the stem tissue of an artichoke infested by the weevil. The nematodes do not feed on plant cells and cannot multiply unless they invade a weevil larva or pupa.

**PARAIOTONCHIOID LIFE CYCLE.** Although similar to that of Allantonematoidea, an important further step in the insect parasitism is taken with the introduction of a parthenogenetic (*Heterotylenchus*, *Paraiontichium*, *Psyllotylenchus*) or secondary heterosexual (*Parasitylenchus*) generation within the insect or mite haemocoel. In the case of *Hetermorphotylenchus*, however, the secondary parthenogenetic female is found in the environment instead of the host haemocoel. This female is non-feeding and produces a few eggs which develop into heterosexual adults which need an insect host for reproduction. A free-living mycetophagous generation with a parthenogenetic female has been described for *Iotonchium californicum* by Poinar (1991), who reported that the mature entomoparasitic female is ovoviviparous and characteristically everts some of its uterine cells from the vulva.

**NEOTYLENCHOID LIFE CYCLE.** This involves a free-living generation capable of feeding and multiplying on fungi or plants, as well as an insect-parasitic phase involving a heterosexual female in the insect haemocoel. *Deladenus* spp. parasitizing siricid woodwasps are typically mycetophagous in free life, and are typically allantonematoid in the insect haemocoel. The eggs of *Deladenus*, containing second-stage juveniles, are deposited by the *Sirex* host simultaneously with its eggs and anthropores of a symbiotic fungus, *Amylostereum*, in the tree tissues. The nematode eggs hatch rapidly and the juveniles feed on the developing hyphae and go on to reproduce as mycetophagous generations. At some stage and in the vicinity of a *Sirex* larva, dimorphic females are produced which have a stylet almost three times as large as usual, and enlarged oesophageal glands. These are fertilized by males with a different spermatogenesis from that of the mycetophagous males, producing hundreds of much smaller sperm. The impregnated females invade the insect larvae by direct penetration of their cuticles.

In the haemocoel of the host larva, the female nematode may attain its full size, several hundred times the original volume, but its reproductive activity begins only after the pupation of the host. Thousands of juveniles are produced in the insect haemocoel by hatching of eggs, ovoviviparity or bursting of the mother's body and these migrate to the host's reproductive organs as the adult woodwasp emerges after pupation. From 50 to 200 juveniles may penetrate an egg, thus arresting its future development, and are deposited when the host oviposits. Those developing in the male woodwasp soon die since they cannot escape (Bedding, 1974).

*Hexatylus viviparus* is similar to *Deladenus* spp. in many respects. In cultures on fungi (e.g. *Alternaria*), it readily grows and multiplies. At some stage, especially in

old cultures, dimorphic impregnated females, similar to those of *Deladenus*, appear (D.J. Hooper, personal communication). The insect host of *Hexatylus* is not known but the life cycle is assumed to be the same as for *Deladenus*.

Instead of feeding on fungi, some Neotylenchoidea have a plant-feeding phase. *Fergusobia* juveniles are deposited in tree shoot tissue, in this case by *Fergusonina* flies on *Eucalyptus* or *Syzygium*. The nematodes feed and multiply parthenogenetically inside the plant gall incited probably by its insect host. Plant parasitism of *Fergusobia* is a means to a direct insect parasitism and not an end in itself. As the host larvae develop inside the gall, numerous infective-stage females are produced which mate with the males appearing at the same time. The impregnated female penetrates the cuticle of the insect larva shortly before its pupation, becoming an adult gravid female by the time the adult fly emerges. Numerous nematode eggs are produced and juveniles migrate to the oviduct to be deposited at the same time as the host's eggs in fresh eucalyptus or jambo shoot tissue.

During my 1960 study on *Gymnotylenchus zeae* Siddiqi, 1961, I found a flourishing phytophagous generation of this nematode within the roots of *Zea mays* L. and on several occasions I noticed some fertilized preadult females with the uterus filled with hundreds of minute sperm and distended into a long sac. The existence of such females and the typical *Hexatylus*-like oesophagus suggest that *Gymnotylenchus* is a Neotylenchoidea. However, the absence of a bursa and a gubernaculum and the small vulva bring it close to forms such as *Heterotylenchus*, in which a free-living generation so far is not known.

*Prothallonema* (syn. *Stictylus*, *Sphaerulariopsis*) spp. have a free-living generation in this group. *Prothallonema intermedium* was maintained in a culture on *Alternaria citri*, in which preadult infective females were produced (Christie, 1938). Study of the type specimens (from the haemocoel of *Dendroctonus monticolus*) of *P. hastatum* (Khan) convinced Siddiqi (1986) that *P. intermedium* and *P. hastatum* were congeneric (see Fig. 145). A free-living generation is not known for *Sphaerularia bombi*. Poinar & Van der Laan (1972) studied the life cycle of *S. bombi* and reported it to be similar to that of the Allantonematoidea as described above. However, the development of *S. bombi* in the presence of fungi has not been observed. I believe that the free-living, fungus-feeding generations of *S. bombi* do exist, since *Sphaerularia* is so similar to *Prothallonema* (= *Sphaerulariopsis*) in morphology and in the evagination of the uterus. In fact, Nickle (1967) stated that *Sphaerulariopsis* might eventually be placed under *Sphaerularia*. In the origin and evolution of parasitism of insect haemocoel several lines can be detected which should help in the classification of Hexatylinea. For example, the flea parasitic nematodes have been assigned to the family Spilotylenchidae which has been classified by Slobodyanyuk (2000) into four subfamilies – Spilotylenchinae, Kurochkinitylenchinae, Psyllotylenchinae and Rubzovinematinae. In this book they are classified differently. Further descriptions of new taxa and knowledge of the life cycles of Hexatylinea will help in a better classification of this large and ancient group.

### Key to superfamilies of Hexatylinea

1. Two alternating entomoparasitic generations in host present; two or more types of adult found in host's haemocoel; spicules may be angular ..... **Iotonchioidea**  
 One entomoparasitic generation present; one type of adult (heterosexual female) present in host's haemocoel; spicules not angular ..... **Sphaerularioidea**

## **SUPERFAMILY SPHAERULARIOIDEA LUBBOCK, 1861 (POINAR, 1975)**

**syn. Neotylenchoidea Thorne, 1941 (Jairajpuri & Siddiqi, 1969)**

### **Diagnosis**

Hexatylna. **Two types of generation, one free-living**, fungus-feeding or plant-parasitic, another involving a heterosexual female parasitic in insect or mite haemocoel, **or free-living fungus-feeding generation cycle absent** or not known (type and many genera). **No complete generation cycle in insect host. Entomoparasitic generation: Only one heterosexual generation with adult parasitic female in insect haemocoel. Preadult female:** Partially free-living. Stylet and oesophageal glands hypertrophied, elongated, extending over intestine or forming a cylinder-like bulb, subventral glands larger than the dorsal gland; only two oesophageal glands that form a short overlap on intestine, reported for type genus. Vulva small, lacking lip flaps. Uterus very long, may extend to middle of body, often packed with hundreds of sperm when impregnated. Ovary under-developed. Tail conoid to subcylindroid. Female penetrates host after impregnation. **Male:** Non-parasitic, occurs in the environment. Essentially similar to free-living female. **Mature female:** In insect haemocoel. Body generally obese and hypertrophied (except in forms with everted uterus). Stylet and oesophagus non-functional; feeding through general body surface or everted uterus. Eversion of uterus takes place in Sphaerulariidae. Everted uterus often hypertrophies into a large sac (= the **uterium**) containing oviduct, ovary and eggs and/or juveniles; female becoming a wrinkled appendage to the uterium. Uterium round to sausage-shaped, 1–20 mm long, capable of absorbing food from haemolymph, and leading an independent life; ovary goes on producing eggs. Juveniles usually develop in host's haemocoel to third or fourth stage and exit from host's anus or vulva for further development, either as a free-living generation or as partially free-living adults, which mate and the impregnated female invades the host. **Free-living generation:** Mycetophagous or plant-parasitic. No sexual dimorphism in anterior region. Cuticle finely annulated or smooth. Lateral fields and deirids generally present; phasmids absent; amphids labial, indistinct in lateral view. Cephalic region low or elevated, smooth, continuous or offset; framework six-, eight- or 12-sectored, lightly to moderately sclerotized. Stylet generally under 20 µm long, base with or without knobs or thickenings. **Oesophagus cylindroid or fusiform, non-muscular, with gland free in body cavity or divisible into corpus, isthmus, and basal bulb region containing glands and usually with a stem-like extension penetrating into intestine. Nerve ring circum-oesophageal or circum-intestinal.** A cellular cardia absent. Excretory pore anywhere between stylet and oesophageal base; excretory duct long, may be sclerotized terminally. Monodelphic, prodelphic. **Female:** Vulva a long transverse slit. Postvulval uterine sac present or absent. Crustaformeria usually in the form of quadricolumella, with four or more cells in each row. Spermatheca axial, elongate. Ovary outstretched, tip may be reflexed due to excessive growth. **Male:** Testis outstretched, with spermatocytes generally serially arranged. Spicules stout, arcuate. Gubernaculum trough-like, fixed, or absent. Bursa present or absent. Tails conoid, cylindroid, or filiform; similar or dissimilar between sexes.



## Type family

Sphaerulariidae Lubbock, 1861

## Other families

Allantonematidae Pereira, 1931

Neotylenchidae Thorne, 1941

## Familia dubia

Paurodontidae Thorne, 1941 (based on free-living forms only; may be a synonym of Sphaerulariidae)

**Key to families of Sphaerularioidea**

1. Entomoparasitic female everts uterus, which often hypertrophies and leads an independent life; oesophageal glands of free-living female form a basal bulb or a short overlap over intestine ..... **Sphaerulariidae**  
Entomoparasitic female does not evert uterus; oesophageal glands of free-living female form a long overlap over intestine ..... **2**
2. Free-living fungus feeding or plant-parasitic generation present  
..... **Neotylenchidae**  
No complete free-living or plant-parasitic generation known  
..... **Allantonematidae**

## Note

The family Neotylenchidae is described here before the Sphaerulariidae, the type family of Sphaerularioidea, because it contains *Hexatylus*, the type genus of the sub-order Hexatyline and a similar sequence was given in the first edition of this book. This family is based on a free-living generation which alternates with an entomoparasitic generation. For some genera of this family and also of the Paurodontidae, here considered as familia dubia, entomoparasitic stages and host are not known.

**Family Neotylenchidae Thorne, 1941****syn. Hexatylidae Skarbilovich, 1952 (Paramonov, 1970)****Fergusobiidae Goodey, 1963 (Siddiqi & Goodey, 1964)****Gymnotylenchidae Siddiqi, 1980****Phaenopsitylenchidae Blinova & Korentchenko, 1986**

## Diagnosis

Sphaerularioidea. **Two types of generation, one free-living, fungus- or plant-feeding**, another involving a heterosexual female parasitic in the insect haemocoel (insect host of adult parasitic female not known for the type genus). **No complete generation cycle in insect host. No sexual dimorphism in anterior region. Entomoparasitic forms: Preadult female:** Partially free-living, fertilized in external environment. Stylet and oesophagus hypertrophied; not suited for feeding on fungi or plants. Ovary immature. Uterus long, packed with minute sperm when impregnated. **Mature female:** In insect haemocoel, not known for *Hexatylus* and *Gymnotylenchus*. Obese, hypertrophied, elongate tuboid or sausage-shaped. **Uterus**

**not everted.** Stylet and oesophagus not functional, food presumably absorbed through general body surface. Reproductive branch much coiled and filling most of body cavity. Oviparous or ovoviviparous. **Free-living, fungus- or plant-feeding forms:** Cuticle smooth or finely striated. Cephalic framework six-, eight- or 12-sectored, lightly to moderately sclerotized. Stylet under 20  $\mu\text{m}$  long; basal knobs may be bifid. Orifice of dorsal gland close to stylet base. Oesophagus cylindroid or fusiform, non-muscular; **basal bulb absent**, glands free in body cavity, extending over intestine. **Nerve ring generally circum-intestinal**, posterior to, or at oesophago-intestinal junction. Excretory pore anterior or posterior to nerve ring. Vulva in posterior region. **Postvulval uterine sac almost always absent.** Monodelphic, prodelphic. Ovary outstretched, may be reflexed secondarily by excessive growth. **Oviduct consisting of two consecutive rings of four cells each in type genus** (*Gymnotylenchinae*). Tail conoid, subcylindroid or cylindroid. Testis outstretched. Bursa present or absent. Spicules small, paired, similar, arcuate, cephalated, distally pointed. Gubernaculum simple, fixed, may be absent (*Gymnotylenchus*, *Fergusobia*).

#### Type subfamily

Neotylenchinae Thorne, 1941

#### Other subfamilies

Fergusobiinae Goodey, 1963

Gymnotylenchinae Siddiqi, 1980

Rubzovinematinae Slobodyanyuk, 1999

#### Key to subfamilies of Neotylenchidae

1. Juveniles and adults of non-entomoparasitic generation partially obese, parasitic in aerial plant galls ..... **Fergusobiinae**  
 Juveniles and adults of non-entomoparasitic generation slender, not parasitic in aerial plant galls ..... **2**
2. Bursa and gubernaculum absent; vulva small, less than half body width long; migratory and parasitic in root tissues in non-entomoparasitic phase ..... **Gymnotylenchinae**  
 Bursa and gubernaculum present; vulva large, half or more of body width long; free-living fungal feeders in non-entomoparasitic phase ..... **3**
3. Cephalic framework eight- or 12-sectored; excretory pore at or posterior to nerve ring; parasites of Diptera ..... **Neotylenchinae**  
 Cephalic framework six-sectored; excretory pore anterior to nerve ring; parasites of Siphonaptera ..... **Rubzovinematinae**

**Subfamily Neotylenchinae Thorne, 1941****syn. Hexatylinae Skarbilovich, 1952****Deladeninae Siddiqi, 1986****Deladeninae Khan, 1969 (= nomen nudum)****Diagnosis**

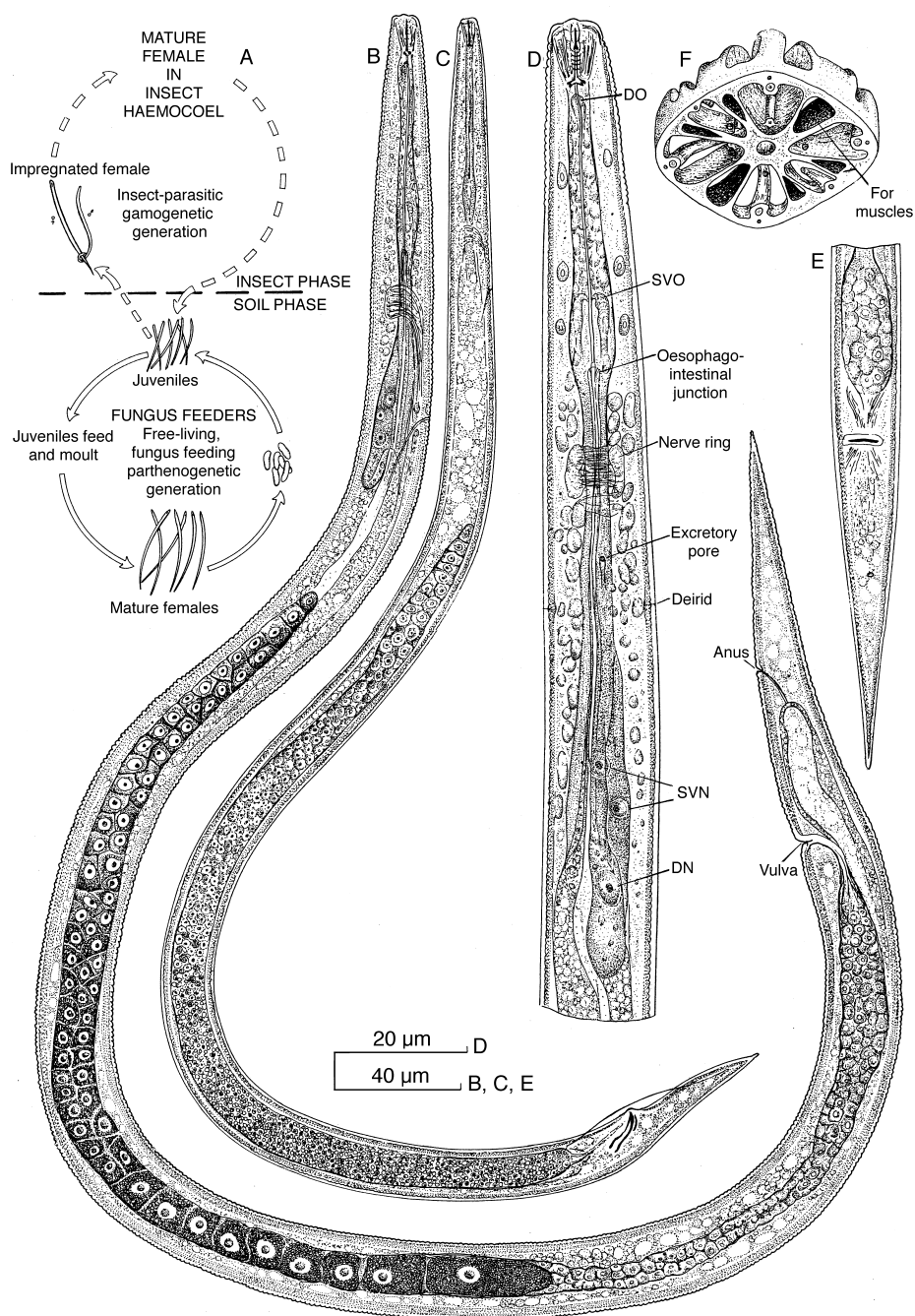
Neotylenchidae. **Adult female** parasitic in insect haemocoel, elongate-obese, tuboid, not dorsally curved. Stylet retracted into body, not functional. Oesophagus and its glands atrophied. **Excretory pore near or behind nerve ring.** Free-living, self-perpetuating generation present, insect host or adult entomoparasitic female not known for type genus. **Free-living forms: Mycetophagous.** Female generally parthenogenetic. **Cephalic framework eight- or 12-sectored.** Stylet knobs bifid in type genus. Oesophageal glands extending over intestine; dorsal gland not abnormally enlarged. Oesophago-intestinal junction anterior to nerve ring. Vulva more than half body width long. **Oviduct with two consecutive rings of four cells each in type genus.** Sperm small. Spicules slender. Gubernaculum present. Bursa large, completely enveloping tail.

**Type genus***Hexatylus* Goodey, 1926**Other genus***Deladenus* Thorne, 1941**Genus *Hexatylus* Goodey, 1926****syn. *Anguillulina* (*Hexatylus* Goodey, 1926) (Schneider 1939)*****Neotylenchus* Steiner, 1931*****Anguillulina* (*Neotylenchus* Steiner, 1931) (Schneider, 1939)*****Scytaleum* Andrásy, 1961**

(Fig. 138)

**Diagnosis**

Neotylenchinae. **Entomoparasitic generation:** Adult female in insect haemocoel, elongate-obese. Males and preadult infective female resembling those of most Sphaerularioidea, female with much larger stylet bearing basal knobs and having enlarged oesophageal glands, extremely elongate uterus filled with minute sperm and immature ovary. Preadult female penetrates an insect host and matures in its haemocoel. **Free-living, mycetophagous generation: Female:** Body vermiform, straight or slightly arcuate ventrally upon relaxation, about 1 mm long (0.76–0.9 mm long, maximum width 45–57  $\mu\text{m}$  in type species). Cuticle finely striated. Lateral fields each with six incisures, not areolated. Cephalic region very low, continuous or slightly offset, smooth; labial disc absent; oral opening circular, six inner labial and four cephalic papillae present; amphid apertures small, labial but slightly posterior to level of cephalic papillae; framework six-sectored at base, **12-sectored anteriorly.** Stylet slender, about 8–12  $\mu\text{m}$  long; conus shorter than shaft; basal knobs in type species duplex or bifid so that they appear as six swellings; two to



**Fig. 138.** *Hexatylus viviparus* Goodey, from a culture on *Alternaria* sp. at Rothamsted Experimental Station, Harpenden, England. A. Life cycle. B. Female. C. Male. D. Oesophageal region of female. DN, dorsal gland nucleus; DO, dorsal gland orifice; SVN, subventral gland nuclei; SVO, subventral gland orifice. E. Tail end of female, ventral. F. Twelve-sectored cephalic framework. (F. After Shepherd *et al.* (1983). Remainder after Siddiqi (1986).)

three guiding rings present around shaft. Some stylet protractors pass through framework to attach to cuticle on top of head. **Oesophagus cylindroid or fusiform.** **Nerve ring circum-intestinal.** Excretory pore behind nerve ring. Oesophageal glands overlapping intestine, dorsal gland larger than subventrals. **Vulva a long transverse slit, usually at less than two body widths from anus.** Vagina directed anteriorly. No postvulval uterine sac. Prodelphic. Uterus with a prominent crustaformeria. Eggs elongate-oval; one or two eggs in uterus at any one time. Oviparous. Oviduct with two consecutive rings of four cells each or two rows of seven to nine cells (Geraert, 1976). Ovary outstretched, tip may be reflexed. Female tail elongate-conoid, pointed, may be filiform. Rectum and anus distinct; **rectum acts as a feeding pump.** **Male: Stylet present.** Testis producing minute rounded sperm. Spicules anteriorly expanded, arcuate, cephalated. Gubernaculum simple, fixed. Bursa distinct, terminal or subterminal. Juveniles essentially similar to female.

### Type species

- Hexatylus viviparus* Goodey, 1926
- syn. *Anguillulina* (*Hexatylus*) *vivipara* (Goodey) W. Schneider, 1939
- Iotonchium viviparum* (Goodey) Filipjev & Schuurmans Stekhoven, 1941
- Neotylenchus abulbosus* Steiner, 1931
- Anguillulina abulbosa* (Steiner) Schneider, 1939
- Hexatylus abulbosus* (Steiner) Goodey, 1933
- Iotonchium abulbosum* (Steiner) Filipjev & Schuurmans Stekhoven, 1941

### Other species

- Hexatylus acutus* (Thorne, 1941) Siddiqi, 1986
- syn. *Neotylenchus acutus* Thorne, 1941 (*N. apiculatus* in Thorne, 1941 = *lapsus calami*)
- H. coprophagus* Goodey, 1938
- syn. *Iotonchium coprophagum* (Goodey) Filipjev & Schuurmans Stekhoven, 1941
- Neotylenchus coprophagus* (Goodey) Thorne, 1941
- H. kirjanovae* (Izatullaeva, 1969) Siddiqi, 1986
- syn. *Neotylenchus kirjanovae* Izatullaeva, 1969
- H. mucronatus* (Izatullaeva, 1969) Siddiqi, 1986
- syn. *Neotylenchus mucronatus* Izatullaeva, 1969
- H. mulveyi* Das, 1964
- H. nudus* (Thorne & Malek, 1968) Siddiqi, 1986
- syn. *Neotylenchus nudus* Thorne & Malek, 1968
- H. vigissi* Skarbilovich, 1952
- syn. *Neotylenchus vigissi* (Skarbilovich) Goodey, 1963
- Scytaleum vigissi* (Skarbilovich) Andr ssy, 1961

### Species inquirendae

- Hexatylus beljaevae* Atakhanov, 1958
- syn. *Neotylenchus beljaevae* (Atakhanov) Andr ssy, 1961
- H. boettgeri* Meyl, 1954
- H. brevicaudatus* Meyl, 1954 (syn. of *H. viviparus* for Meyl, 1961)
- H. dipapillatus* Meyl, 1954 (syn. of *H. viviparus* for Meyl, 1961)

- H. italicus* (Meyl, 1954) Ebsary, 1991  
 syn. *Neotylenchus italicus* Meyl, 1954  
*Scytaleum italicum* (Meyl) Andr  ssy, 1961
- H. longicauda* (Kozłowska, 1970) Ebsary, 1991  
 syn. *Neotylenchus longicauda* Kozłowska, 1970
- H. obesus* (Thorne, 1934) Ebsary, 1991  
 syn. *Neotylenchus obesus* Thorne, 1934  
*Iotonchium obesus* (Thorne) Filipjev & Schuurmans Stekhoven, 1941
- H. skarbilowiezae* Atakhanov, 1958  
 syn. *Scytaleum skarbilowiezae* (Atakhanov) Andr  ssy, 1961  
*Neotylenchus skarbilowiezae* (Atakhanov) Goodey, 1963
- H. thornei* (Meyl, 1954) Ebsary, 1991  
 syn. *Neotylenchus thornei* Meyl, 1954  
*Scytaleum thornei* (Meyl) Andr  ssy, 1961
- H. velatus* (B  tschli, 1873) Ebsary, 1991  
 syn. *Tylenchus velatus* B  tschli, 1873  
*Anguillulina velata* (B  tschli) Goodey, 1932  
*Iotonchium velatum* (B  tschli) Filipjev & Schuurmans Stekhoven, 1941  
*Neotylenchus velatus* (B  tschli) Skarbilovich, 1952 (note: probably a *Nothotylenchus*)
- H. zae* (Schuurmans Stekhoven in Filipjev & Schuurmans Stekhoven, 1941) Ebsary, 1991  
 syn. *Iotonchium zae* Schuurmans Stekhoven in Filipjev & Schuurmans Stekhoven, 1941  
*Neotylenchus zae* (Schuurmans Stekhoven in Filipjev & Schuurmans Stekhoven) Skarbilovich, 1952

#### Nomen nudum

*Hexatylus galatea* Izatullaeva, 1967

#### Note

Nickle (1968) synonymized *Neotylenchus* Steiner and *Scytaleum* Andr  ssy with *Hexatylus*. All the nominal species may involve a parasitic cycle in the haemocoels of insects or mites.

ETYMOLOGY. From Greek *hex* = six, and *tylos* = knot, knob.

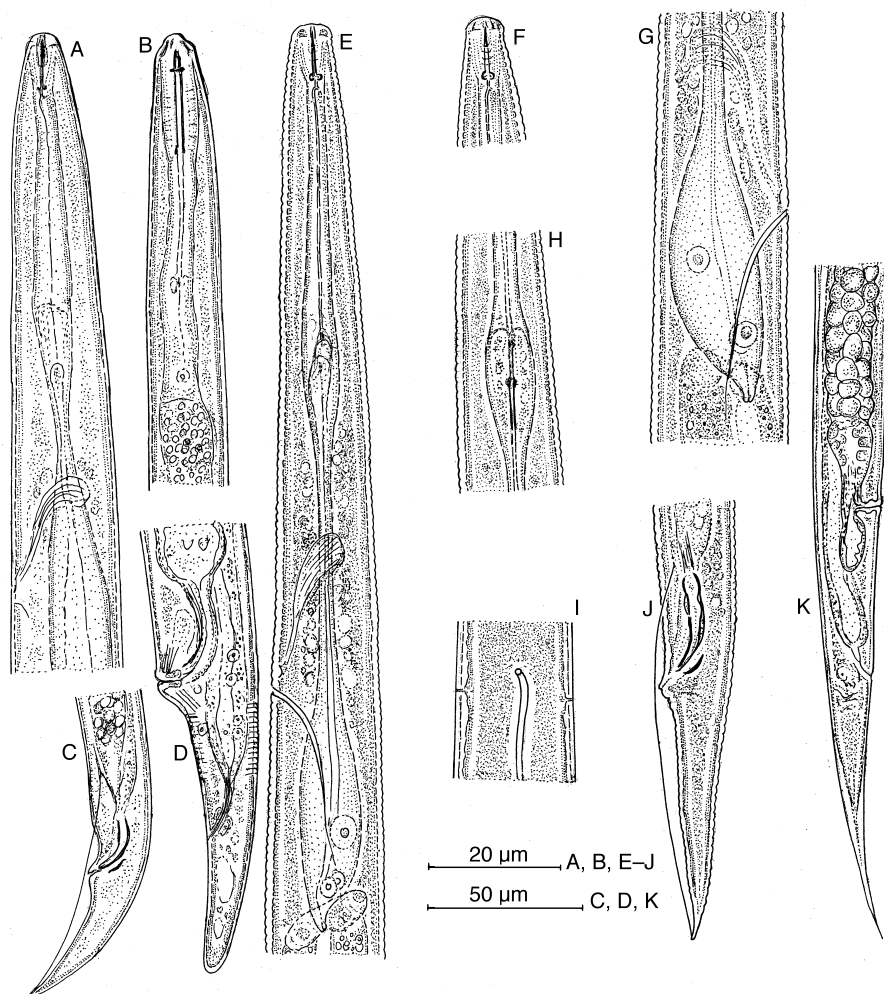
The type species was found in a diseased potato tuber and gladiolus corms in England. It is parthenogenetic and contrary to its name, is oviparous. It is easily maintained on fungus in culture. Occasionally dimorphic preadult females with a larger stylet and oesophageal glands appear in the culture (D.J. Hooper, personal communication).

**Genus *Deladenus* Thorne, 1941**syn. *Hadrodenus* Mulvey, 1969 (? gen. inq.)*Dotylaphus* Andrásy, 1958*Physitylenchus* Rao & Reddy, 1982*Beddingia* Blinova & Korentchenko, 1986*Phaenopsitylenchus* Blinova & Korentchenko, 1986

(Fig. 139, A–D)

**Diagnosis**

Neotylenchinae. **Entomoparasitic generation: Mature female:** In insect haemocoel. Elongate-obese, tuboid, 3–15 mm long, 100–500  $\mu\text{m}$  wide; metabolic products slightly greenish. Cephalic region overgrown by body enlargement. Stylet retracted into body. Oesophagus and its glands degenerate. **Preadult female:** Partially free-living. Body 0.88–1.74 mm long. Lateral fields with 8–14 incisures near middle of body, not repeatedly branching as in the mycetophagous female. Stylet hypertrophied, very stout, with wide lumen, lacking distinct knobs, 14–30  $\mu\text{m}$  long. Oesophageal glands and their ducts also hypertrophied; **subventral glands enlarged**. Orifices of glands with fan-like collecting tubules; dorsal gland orifice about one stylet length behind stylet base; orifices of subventral glands a little less than halfway between nerve ring and orifice of dorsal gland. Excretory pore just anterior, opposite or just posterior to nerve ring. Vulva a small transverse slit; lips not protuberant. Vagina thick-walled. A short postvulval uterine sac is secondarily formed when uterus is distended with sperm. Uterus with spermatheca elongated and packed with minute (1–2  $\mu\text{m}$  in diameter) sperm, may become about half as long as body. **Male:** Similar to that of the mycetophagous generation, but the testis produces hundreds of minute sperm 1–2  $\mu\text{m}$  in diameter. **Free-living generation: Female:** About 1–2 mm long, **very slender** ( $a = 40\text{--}60$ ) in young, slightly swollen in older females, straight or ventrally curved when relaxed. Cuticle finely striated. Lateral field with 6–15 incisures. Cephalic region low, smoothly rounded; framework eight-sectored, lightly sclerotized. **Stylet small** (usually 8–10  $\mu\text{m}$ ), with distinct basal knobs. Orifice of dorsal gland close behind stylet base. Oesophagus non-muscular, cylindroid with slight basal expansion in region of orifices of subventral glands. **Oesophago-intestinal junction at or anterior to nerve ring. Dorsal gland enormous**, extending on dorsal side of intestine; **subventrals reduced**. Excretory pore generally near nerve ring but may be posterior to it, anterior or posterior to hemizonid. Deirids near excretory pore. Intestine with distinct lumen. Rectum and anus distinct. **Vulva extremely posterior, generally at 93–94% of body length, at less than vulval body width from anus. No postvulval uterine sac.** Spermatheca elongate axial, with large (10–12  $\mu\text{m}$ ) sperm when spermated. Oviduct consisting of two rows of seven to nine cells each (Geraert, 1976). Ovary long, outstretched, oocytes in one or two rows. Columella with four rows of four cells each. One or two eggs in uterus at one time, occasionally several eggs occur in old females. Tail subcylindroid, conoid or conoid-rounded. **Male:** Body slender; size, stylet and oesophagus as in mycetophagous female. Spicules moderately robust, anteriorly broad, arcuate, generally 16–22  $\mu\text{m}$  (24–38  $\mu\text{m}$  in *D. proximus*) long. Gubernaculum trough-shaped, fixed. Tail conoid, completely enveloped by a prominent bursa. Testis outstretched; sperm large 10–12  $\mu\text{m}$  in diameter as in impregnated mycetophagous females.



**Fig. 139.** A and B. *Deladenus siricidicola* Bedding, paratypes. C and D. *Deladenus* sp. From Adelaide, Australia. E–K. *Paurodontoides linfordi* (Hechler) from a culture sent by Hechler. B. Entomoparasitic preadult female, remainder fungus feeders. C and J. Male tails; remainder females. A and E. Oesophageal regions. B and F. Head ends. G and H. Basal bulb and postcorpus, respectively. I. Excretory pore and deirids in ventral view. D and K. Posterior regions of females.

### Hosts

Hymenoptera: *Ibelia*, *Sirex*, *Urocerus*, *Xeris*.  
Coleoptera: *Serropalpus*.

### Type species

*Deladenus durus* (Cobb, 1922) Thorne, 1941  
syn. *Tylenchus durus* Cobb, 1922  
*Anguillulina dura* (Cobb) Goodey, 1932



*Ditylenchus durus* (Cobb) Filipjev, 1936  
*Deladenus andrassyi* Vinciguerra, 1972  
*Deladenus paradurus* Massey, 1974

### Other species

*Deladenus aenea* (Rao & Reddy, 1982) Ebsary, 1991  
 syn. *Physitylenchus aenea* Rao & Reddy, 1982  
*D. apopkaetus* Chitambar, 1991  
*D. arboricola* (Cobb, 1922) Goodey & Franklin in Goodey, 1956 (sp. inq. for Chitambar, 1991)  
 syn. *Tylenchus arboricola* Cobb, 1922  
*Anguillulina arboricola* (Cobb) Goodey, 1932  
*Ditylenchus arboricola* (Cobb) Filipjev & Schuurmans Stekhoven, 1941  
*D. aridus* Andr  ssy, 1957  
 syn. *Deladenus crassus* Zell, 1985  
*D. indicus* Singh, 1976  
*D. ipini* Massey, 1974  
*D. laricis* (Blinova & Korentchenko, 1986) Ebsary, 1991  
 syn. *Phaenopsitylenchus laricis* Blinova & Korentchenko, 1986  
*D. minimus* Chizhov & Sturhan, 1998  
*D. nevexii* Bedding, 1974  
 syn. *Beddingia nevexii* (Bedding, 1974) Blinova & Korentchenko, 1986  
*D. norimbergensis* R  hm, 1956  
*D. obesus* Thorne, 1941  
*D. pakistanensis* Shahina & Maqbool, 1992  
*D. parvus* Zell, 1985  
*D. ulani* Sultanalieva, 1983

### Superspecies

*D. siricidicola* Bedding, 1968 (Chitambar, 1991), with the following species:  
*D. (siricidicola) siricidicola* Bedding, 1968  
 syn. *Beddingia siricidicola* (Bedding) Blinova & Korentchenko, 1986  
*D. (siricidicola) canii* Bedding, 1974  
 syn. *Beddingia canii* (Bedding) Blinova & Korentchenko, 1986  
*D. (siricidicola) imperialis* Bedding, 1974  
 syn. *Beddingia imperialis* (Bedding) Blinova & Korentchenko, 1986  
*D. (siricidicola) rudyi* Bedding, 1974  
 syn. *Beddingia rudyi* (Bedding) Blinova & Korentchenko, 1986  
*D. wilsoni* Bedding, 1968 (Chitambar, 1991), with the following species:  
*D. (wilsoni) wilsoni* Bedding, 1968  
 syn. *Beddingia wilsoni* (Bedding) Blinova & Korentchenko, 1986  
*D. (wilsoni) proximus* Bedding, 1974  
 syn. *Beddingia proximus* (Bedding) Blinova & Korentchenko, 1986

### Species inquirendae

*Deladenus lonchites* (Massey, 1974) Fortuner & Raski, 1987  
 syn. *Dotylyphus lonchites* Massey, 1974

*Deladenus ruehmi* (Andrássy, 1958) Fortuner & Raski, 1987  
syn. *Dotylaphus ruehmi* Andrásy, 1958

## Remarks

*Deladenus* spp. have free-living amphimictic generations feeding on fungi and a parasitic heterosexual cycle in which the female becomes dimorphic, with hypertrophy of the stylet and subventral oesophageal glands, and is impregnated before parasitizing the haemocoel of insects (usually the woodwasps, *Sirex* spp., Siricidae). The *Sirex* parasitism was discovered by Zondag (1962) in New Zealand and the life history, involving two cycles, was reported by Bedding (1967). Mycetophagous stages of various species of *Deladenus* were described and their taxonomy discussed by Chitambar (1991), who synonymized the genus *Beddingia* Blinova & Korentchenko, 1986, with *Deladenus*. *Physitylenchus* Rao & Reddy, 1982 and *Phaenopsitylenchus* Blinova & Korentchenko, 1986, are based on type species which cannot be differentiated from those of *Deladenus* and are here considered as junior synonyms of *Deladenus*.

The Siricidae are parasitized throughout Europe, Asia and Australia. *Deladenus siricidicola* is now being used as an agent for biological control of *Sirex noctilio* F. which, with the aid of a phytotoxic mucus and a symbiotic fungus, *Amylostereum areolatum*, is able to kill pine trees (*Pinus radiata*) in Australia (Bedding, 1984). The nematode has survived on *Amylostereum areolatum* for more than 12 years with nearly 200 generations without the intervention of an insect-parasitic cycle (Bedding, 1984). When cultured on *Amylostereum*, *D. canii* juveniles become adults within 5 days at 22°C. Mating takes place and the female lays 300–800 eggs in 2–3 weeks. The eggs hatch in 3–4 days and the juveniles feed and grow on the fungus (Bedding, 1974).

In monoxenic cultures, the juveniles become mycetophagous females, or males with large sperm, but when the cultures age or become contaminated with bacteria, infective females and males with small sperm are produced (Bedding, 1984). In contrast to the mycetophagous females, the non-feeding infective females have a rudimentary dorsal gland, but abnormally enlarged subventral glands which aid in the penetration of the insect host cuticle. The stylet is hypertrophied and has a swollen base or, as in *D. minimus*, well-developed knobs.

The *Deladenus* spp. are highly specific to fungal species and appear to have co-evolved with them. Both nematode and fungus use *Sirex* spp. for simultaneous transportation to un-infested trees. *Deladenus siricidicola* and *D. wilsoni* feed upon *Amylostereum areolatum*, but other species that parasitize siricids utilize only *A. chailettii* to complete the mycetophagous life cycle. The *Sirex* female oviposits nematode-filled eggs, along with spores of the symbiotic fungus and mucus, into the trees. The rapidly growing fungus is utilized as food by both nematodes and siricid larvae. The nematodes grow and multiply under the bark and within the tracheids and resin canals, competing significantly for food with the siricid larvae; the latter do not grow as large as those in uninfected trees (Bedding, 1984).

*Dotylaphus* was based on the infective preadult heterosexual female which may belong to *Deladenus*, *Prothallonema* or one of the several genera of Allantonematidae. It has been synonymized with *Deladenus* but was regarded as

genus *dubium* by Siddiqi (1986). A key to *Deladenus* spp. is given by Chitambar (1991).

ETYMOLOGY. From Greek *delos* = visible, and *aden* = gland, modified to masculine gender.

*Deladenus durus* was found in galls of chestnut oak, *Quercus prinus* L., in Virginia, USA, apparently feeding on associated fungi. It was found in association with a decaying fungus, *Pleurota* sp., and in the soil around alfalfa crowns in Utah and is believed to be a fungus-feeder (Thorne, 1941, 1961). It was also found in grass soil on Ellesmere Island, Canadian Arctic.

## Subfamily Gymnotylenchinae Siddiqi, 1980

### Diagnosis

Neotylenchidae. Cephalic region offset, low, finely striated; **framework eight-sectored**. Oesophagus cylindroid, non-muscular; glands overlapping intestine. Oesophago-intestinal junction anterior to nerve ring. **Vulva a small slit**, less than half body width long. Prodelphic. Postvulval uterine sac absent. Tails similar in both sexes, elongate-subcylindroid in type genus. **Bursa and gubernaculum absent**. Spicules prominently cephalated. Probably parasitic in roots, suspected of having an entomoparasitic generation.

### Type genus

*Gymnotylenchus* Siddiqi, 1961

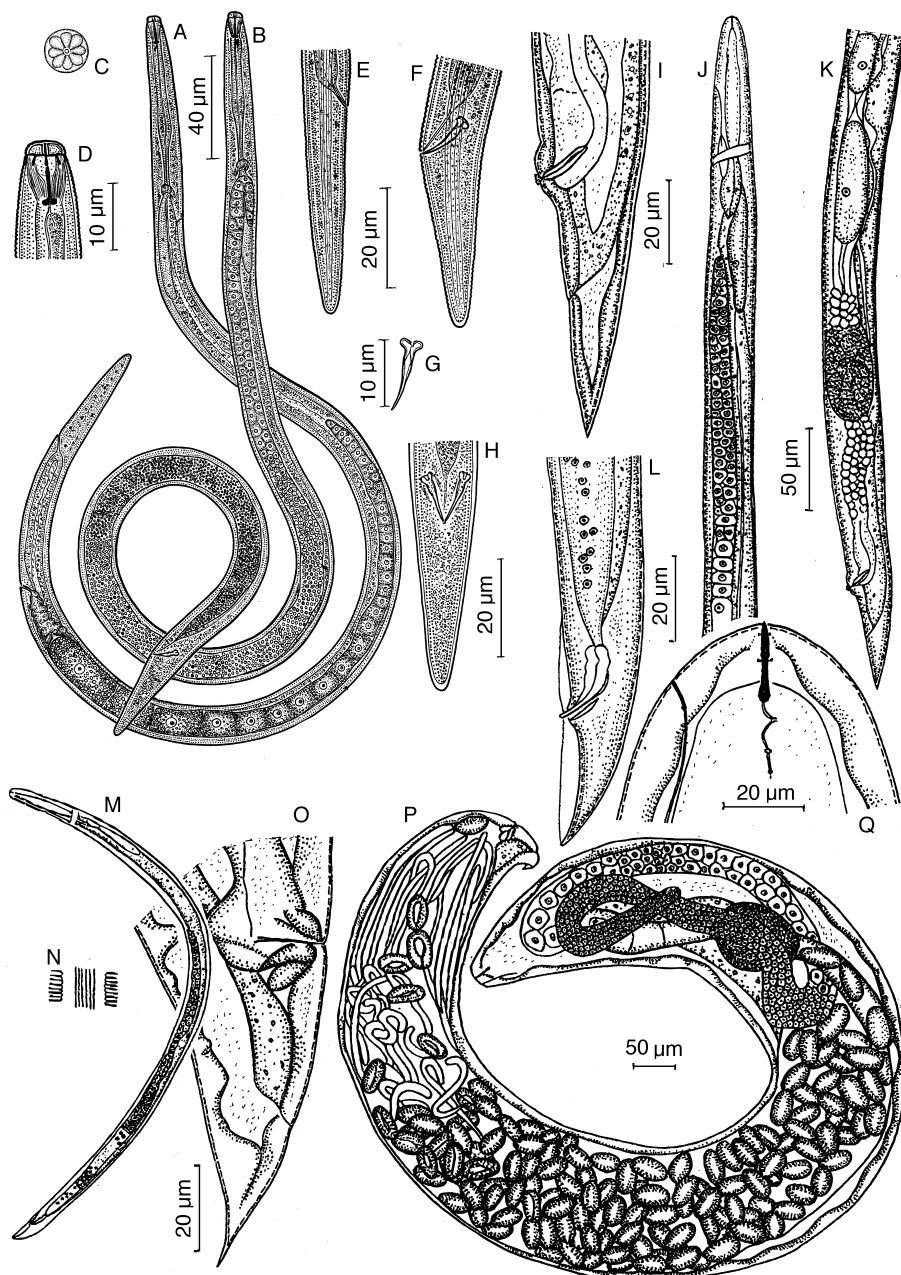
No other genus.

## Genus *Gymnotylenchus* Siddiqi, 1961

(Fig. 140, A–H)

### Diagnosis

Gymnotylenchinae. **Adults found inside roots**; body straight to ventrally arcuate when relaxed; 0.48–0.63 mm long;  $a = 34\text{--}43$  in type species. Cuticle finely striated. Lateral field with six incisures. Stylet moderately strong, small (8–11  $\mu\text{m}$  long in type species); knobs distinctly rounded. Oesophagus cylindroid, with a non-valvate swelling in region of orifices of subventral glands. Orifice of dorsal oesophageal gland closely behind stylet base. **Oesophago-intestinal junction anterior to nerve ring**. Oesophageal glands forming an elongate diverticulum extending over intestine dorsally or subdorsally. Excretory pore behind nerve ring. Vulva small, transversely oval, pore-like, at 80–84% of body length in type species. Vagina directed forward. A quadricolumella of 16 cells present. Spermatheca not formed. Vulva–anus distance a little more than tail length in type species. Intestine with distinct lumen throughout. Rectum and anus distinct. Female tail elongate-subcylindroid, with a rounded smooth terminus. **Entomoparasitic generation**: Preadult, impregnated infective females seen but not described by Siddiqi (1961). Male tail similar to that of free-living female, but slightly directed dorsally. Vas deferens packed with minute



**Fig. 140.** A–H. *Gymnотylenchus zeae* Siddiqi. Free-living generation found in plant roots. A. Female. B. Male. C. *En face* view of female. D. Head end of male. E. Tail end of female. F and H. Tail ends of male, lateral and ventral view, respectively. G. Spicule. I–Q. *Rubzovinema ceratophyllus* Slobodyanyuk. I and L. Tail ends of female and male of free-living generation, respectively. J and K. Anterior and posterior regions of free-living female, respectively. M. Free-living male. N. Lateral field. O and Q. Postvulval and head region of mature entomoparasitic female, respectively. P. Mature entomoparasitic heterosexual female. (A–H. After Siddiqi (1961), courtesy *Nematologica*. I–Q. After Slobodyanyuk (1991), courtesy *Zoologicheskyy Zhurnal*.)

sperm numbering several hundreds. Testis outstretched with tip sometimes reflexed, reaching oesophagus, with spermatocytes in one or two rows. **No trace of bursa or gubernaculum.** Spicules prominently cephalated, distally pointed.

#### Type species

*Gymnotylenchus zae* Siddiqi, 1961

#### Other species

*Gymnotylenchus dendrophilus* (Rühm, 1956) Sumenkova, 1975

syn. *Neotylenchus dendrophilus* Rühm, 1956

*G. fusiformis* Truskova & Eroshenko, 1977

#### Remarks

The oesophagus and the male tail of *Gymnotylenchus* are similar to those in free-living forms of some entomoparasitic genera (*Heterotylenchus*, *Protylenchus*) and the vulva is small as in several genera of Hexatyline, including *Sphaerularia*. The occurrence of only juveniles of *G. zae* in large numbers and fertilized preadult females in some root samples observed by Siddiqi (1961) suggests that at some stage the nematodes attack an insect associated with the host plants.

ETYMOLOGY. Greek *gymnos* = naked (due to the absence of a bursa), and *Tylenchus*.

The type species was found inside roots of *Zea mays* L. and *Sorghum vulgare* Pers. at Aligarh, India.

### Subfamily Fergusobiinae Goodey, 1963

#### Diagnosis

Neotylenchidae. **With two types of life cycle, one plant-parasitic generation in aerial plant galls** involving parthenogenetic females and the other with heterosexual female parasitic in insect haemocoel. Four types of adults: shoot gall-parasitic parthenogenetic female, gall-inhabiting male, preadult heterosexual infective female, and heterosexual entomoparasitic female. **Juveniles, females and males in plant gall partially obese. Cephalic framework six- or eight-sectored.** Stylet knobbed. Oesophagus broad, fusiform; oesophago-intestinal junction anterior to nerve ring. Oesophageal glands bulboid, extending over intestine; dorsal gland enormously developed. Vulva a large transverse slit. Spicules moderately robust. **Gubernaculum absent.** Bursa well developed. Type genus parasitic in haemocoel of *Fergusonina* spp. and in plant shoot-galls of *Eucalyptus* and *Syzygium* spp.

#### Type genus

*Fergusobia* Currie, 1937

No other genus.

#### Remarks

This subfamily, containing only the genus *Fergusobia*, is interesting in that both the insect-parasitic and plant gall-inhabiting forms, including the juveniles and males, are obese. Throughout the order Tylenchida, the males are slender and capable of

serpentine movement, except in *Anguina*, in which they are semi-obese. The obesity of males in *Fergusobia* and *Anguina* may be primarily due to the limited space for movement within the gall and because the males are only partially migratory (cf. *Meloidogyne*, where the males are migratory).

*Fergusobia* spp. show dual parasitism of agromyzid flies (*Fergusonina* spp.) and aerial shoot-galls of *Eucalyptus* spp. in Australia and of *Syzygium cumini* in India. The fly deposits its eggs with nematode juveniles in plant tissue and soon the juveniles develop into parthenogenetic females. Fisher & Nickle (1968) observed that gall formation begins before the insect eggs hatch. Thus the fly seemingly injects a gall-inciting substance during oviposition.

In the gall, nematodes have a protected environment with abundant food. Here the parthenogenetic female feeds, presumably on plant cells, and lays eggs. The hatched juveniles feed and become obese since they do not migrate onto or within the gall to initiate a new feeding site. **Their goal is parasitism of insects, not the continuing parasitism of the plant.** At about the time fly larvae reach the third instar, infective-stage females and males are produced, which mate in the gall, where the impregnated females find and penetrate the insect larvae. During pupation, the nematodes (up to seven in number) grow rapidly in the fat body of the pupa and, by the time the adult fly emerges, become adult gravid females. The eggs hatch in the fly haemocoel, and the juveniles migrate to the oviduct to be deposited by the female with its eggs in fresh plant tissue (Fisher & Nickle, 1968). Thus, the transportation of the nematode to a fresh plant gall is not by active migration, which would require a vermiform stage, but passively through an insect host.

**Genus *Fergusobia* Currie, 1937 (Christie, 1941)**

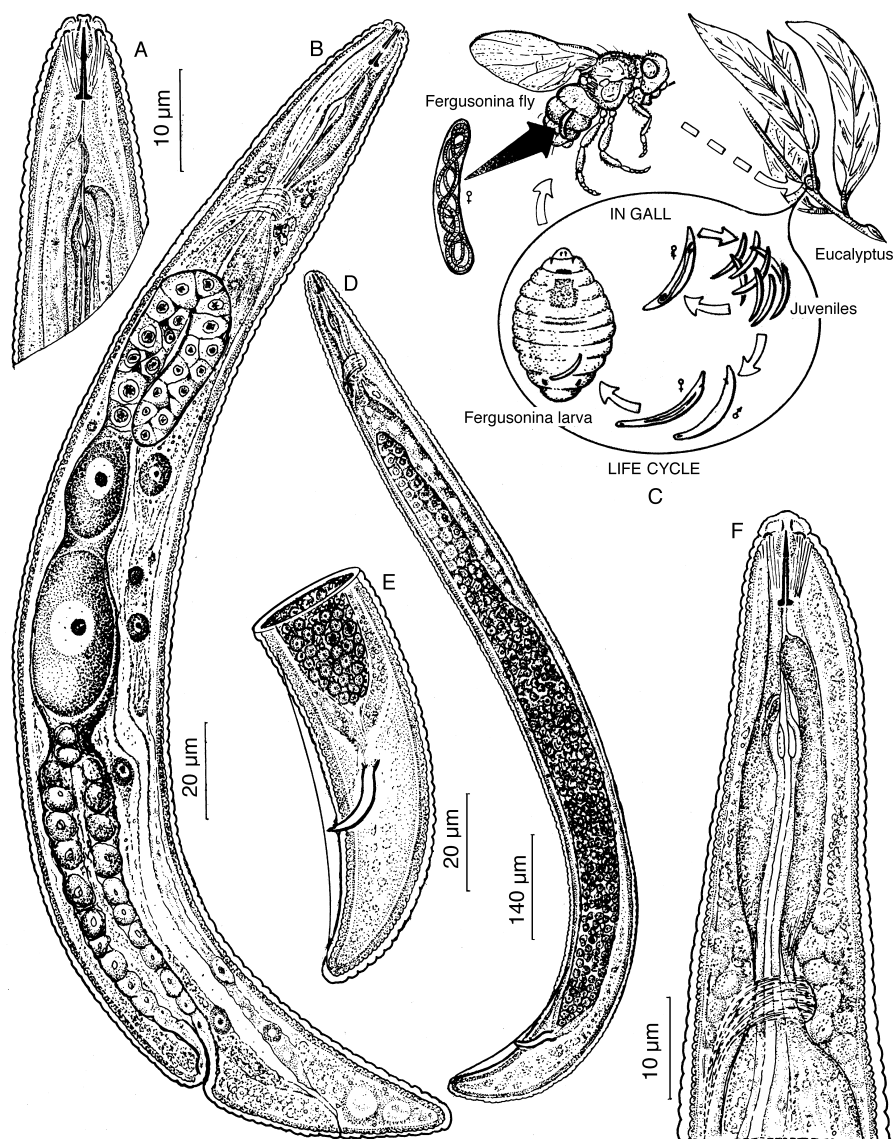
**syn. *Anguillulina* (*Fergusobia* Currie, 1937)**

***Dorsalla* Jairajpuri, 1966**

(Figs 8(d), D; 141)

**Diagnosis**

Fergusobiinae. **Non-entomoparasitic forms: In galls on shoots of trees associated with agromyzid flies. Female:** Generally parthenogenetic. Body semi-obese, elongate spindle- or sausage-shaped, **dorsally curved** (with ventral side convex) when relaxed, about 1 mm or less long (0.415 mm long in type species). Cuticle finely striated. Lateral fields usually with four incisures. Cephalic region smooth, continuous or slightly offset, central region may be elevated like a cone in some species; **framework six- or eight-sectored**; lightly sclerotized. Stylet short, 5–12  $\mu\text{m}$  long (Currie (1937) reported female and male stylets of *F. tumifaciens* to be 19  $\mu\text{m}$  and 12  $\mu\text{m}$  long, respectively), with symmetrical, round or flanged basal knobs. Orifice of dorsal gland near stylet base. Corpus large, oval or cylindroid. Oesophageal glands large, elongated, extending over intestine. **Oesophago-intestinal junction anterior to nerve ring.** Nerve ring circum-intestinal, at base of corpus (isthmus absent). Excretory pore posterior to nerve ring. Vulva a prominent transverse slit, at about 75–85% of body length; lips raised. Prodelphic; no postvulval uterine sac. Ovary outstretched, sometimes reflexed due to excessive growth; oocytes usually in single file. Tail conoid-rounded, 39  $\mu\text{m}$  long in type species. Rectum and anus distinct. Generally oviparous, eggs laid in plant galls, where they hatch, the juveniles devel-



**Fig. 141.** *Fergusonobia tumifaciens* (Currie) from *Eucalyptus* shoot-gall in Adelaide, Australia. A. Head end of female. B. Female. C. Life cycle. D. Male. E. Tail end of male. F. Anterior region of female.

oping either into parthenogenetic females or into males and infective-stage females. **Infective-stage heterosexual female:** Slightly larger, slimmer than but essentially similar to the parthenogenetic female. Uterus acts as extensile spermatheca, extending from vagina to base of oesophageal glands. Ovary and oviduct with flexures. Vulva inconspicuous; lips not elevated. Prominent intestinal and hypodermal nuclei

present. Tail broadly rounded. **Juveniles:** **Body partially obese**, stylet and oesophagus as in female. **Male:** **Partially obese**, posterior region ventrally arcuate. No sexual dimorphism in stylet or oesophagus. Vas deferens extensive, packed with minute, round sperm. Testis reaching oesophagus. **Spicules robust, angular. Gubernaculum absent.** Bursa enveloping tail. **Entomoparasitic female:** In insect haemocoel. Sausage-shaped or elongate tuboid, 0.77–0.95 mm long, 16–21 µm wide in type species. Cephalic region overgrown by body expansion. Stylet knobbed, in normal position. Oesophagus, rectum and anus degenerate. Vulva an enlarged depressed slit at about 77–88% of body length. Ovary coiled, filling most of body cavity; oocytes arranged about a rachis. Spermatheca with minute sperm. Oviparous. Eggs hatch in insect haemocoel and juveniles migrate to insect oviduct to be deposited in plant tissue with the insect eggs during oviposition.

### Host

Diptera (Acalyptrate family Agromyzidae): *Fergusonina*.

### Type species

*Fergusobia tumifaciens* (Currie, 1937) Wachek, 1955

syn. *Anguillulina* (*Fergusobia*) *tumifaciens* Currie, 1937

*Anguillulina* (*Fergusobia*) *curriei* Johnston, 1938 (was a nom. nov.)

*Fergusobia curriei* (Johnston, 1938) Christie, 1941 (nec *Anguillulina tumefaciens* (Cobb, 1932) T. Goodey, 1933 = *Tylenchus tumefaciens* Cobb, 1932)

### Other species

*Fergusobia brevicauda* Siddiqi, 1996

*F. fisheri* Davies & Lloyd, 1996

*F. indica* (Jairajpuri, 1962) Siddiqi, 1986

syn. *Boleodorus indicus* Jairajpuri, 1962

*Dorsalla indica* (Jairajpuri) Jairajpuri, 1966

*F. jambophila* Siddiqi, 1986

*F. magna* Siddiqi, 1986

*F. philippinensis* Siddiqi, 1996

### Remarks

*Anguillulina* (*Fergusobia*) *tumifaciens* Currie, 1937 is neither a primary homonym of nor congeneric with *Tylenchus tumefaciens* Cobb (notice difference in spelling), and hence the replacement name *A. (F.) curriei* proposed for it by Johnston (1938) is not valid. Although Article 59 (b)(i) of ICZN provides for preserving secondary homonyms that existed before 1961, the name *Fergusobia tumifaciens* was used before 1961 by Wachek (1955) and later by Baker (1962), Goodey (1963) and Nickle (1967). Hence the resurrection of *F. curriei* (Johnston) by Fisher & Nickle (1968) is not justified.

ETYMOLOGY. From its type host's name *Fergusonina*, and Greek *bios* = life, living in.

The type species was found in leaf-galls of *Eucalyptus Stuartiana* formed by *Fergusonina carteri* Tonnoir and in the body cavity of *Fergusonina carteri*. *Fergusobia indica* was found by Jairajpuri (1966a) around roots of *Allium cepa* L. at Aligarh,



India, in a tree-filled park. Repeated attempts to collect the nematode at the type locality failed. Two females collected by Dr E. Khan at Aligarh from near the trees were examined and found to be conspecific with *F. indica*.

The species reported by Harris (1982, *Syst. Entom.* 7, 211–216) from jambo tree (*Syzygium cumini* (L.)) shoot-galls formed by *Fergusonina syzygii* Harris, from Hyderabad, India, was described as *F. jambophila* by Siddiqi (1986b) and a species collected by Siddiqi in 1983 from shoot-galls of *Eucalyptus* at Brisbane, Australia was described as *F. magna*. *Fergusobia fisheri* was described from leaf-galls of a hybrid of *Eucalyptus leucoxylon* in association with *Fergusonina* flies in South Australia (Davies & Lloyd, 1996). Two other species, *Fergusobia brevicauda* Siddiqi, 1996 and *F. philippinensis* Siddiqi, 1996, were described by Siddiqi (1996) from *Eucalyptus deglupta* in Papua New Guinea and the Philippines, respectively. The descriptions of these species appeared in 1994 in the Proceedings of the Afro-Asian Nematology Symposium held at the Menoufiya University but these Proceedings were later withdrawn due to bad quality of printing and some of the papers in it, including Siddiqi's, were reprinted in 1996.

A key to *Fergusobia* spp. was given by Siddiqi (1986b).

## Subfamily Rubzovinematinae Slobodyanyuk, 1999

### Diagnosis

Neotylenchidae. **Life cycle with alternation of entomoparasitic heterosexual and free-living heterosexual generations.** Adult female parasitic in insect haemocoel, obese, dorsally curved, crescent-shaped or spiral. Stylet with slight basal swellings, not retracted into body. Oesophagus and its glands atrophied. **Excretory pore anterior to nerve ring, opposite stylet base.** Tail conoid-pointed, dorsally curved. Spermatheca present. Uterus voluminous, sac-like, containing numerous eggs and juveniles in mature females. **Ovoviviparous. Free-living forms:** Free-living, heterosexual generation present in flea nest, feeding on associated fungi. Female elongate, slender. Stylet thin and short (about 10  $\mu\text{m}$ ). Excretory pore anterior to nerve ring. Spermatheca filled with minute sperm. Male elongate, slender. Sperm small. Spicules slender. Gubernaculum present. Bursa enveloping tail.

### Type genus

*Rubzovinema* Slobodyanyuk, 1991

No other genus.

## Genus *Rubzovinema* Slobodyanyuk, 1991

(Fig. 140, I–Q)

### Diagnosis

Rubzovinematinae. Alternation of two heterosexual generations present, one entomoparasitic, other free-living. **Entomoparasitic generation:** Adult female parasitic in flea haemocoel, obese, dorsally curved, crescent-shaped or spiral, 0.81–1.84 mm long ( $a = 6.4$ – $16.8$ ) in type species. Stylet 18–21  $\mu\text{m}$  long, with slight basal swellings, not retracted into body. Anterior end of body rounded. Oesophagus degenerate. **Excretory pore anterior to nerve ring, opposite stylet base.** Tail

conoid, with pointed tip, dorsally curved. Vulva at 95–99% of body length. Ovary with two to three flexures, in anterior half of body. Spermatheca large, rounded, filled with minute (diam.  $< 1 \mu\text{m}$ ) sperm. Uterus occupying one half to two-thirds of body volume, containing eggs and juveniles in mature females. **Ovoviviparous.** **Free-living forms: Free-living, heterosexual generation present in flea nest,** feeding on associated fungi. **Female:** Body vermiform, 0.64–0.79 mm long ( $a = 19.8\text{--}32.8$ ) in type species. Stylet thin, 8–9  $\mu\text{m}$  long, with minute basal knobs. Oesophagus cylindroid to elongate-spindle-shaped. Oesophageal glands extending over intestine. Excretory pore anterior to nerve ring, duct leading into renette located at level of nerve ring. Vulva at 83.3–92.5% of body in type species; lips protuberant; vulva–anus distance about as long as tail. Ovary with oocytes in one or two rows, extending to oesophageal gland region. Spermatheca large, oval, filled with minute sperm. Tail conical, with pointed tip. Oviparous. **Male:** Elongate, slender, about as long as female. Stylet (9–10  $\mu\text{m}$  long) and oesophagus as in female. Testis outstretched; sperm small. Spicules slender. Gubernaculum present, linear. Bursa distinct, enveloping tail which is conoid and ventrally arcuate.

#### Host

Siphonaptera: *Citellophilus*.

#### Type species

- Rubzovinema ceratophyllus* (Rubzov & Samurov, 1981) Slobodyanyuk, 1991  
 syn. *Psyllotylenchus ceratophyllus* Rubzov & Samurov, 1981  
*Psyllotylenchus acuticauda* Rubzov & Tshumakova, in Rubzov, 1981  
*Rubzovinema acuticauda* (Rubzov & Tshumakova, in Rubzov) Slobodyanyuk, 1991  
*Psyllotylenchus acuticephalus* Rubzov & Tshumakova, in Rubzov, 1981  
*Rubzovinema acuticephalus* (Rubzov & Tshumakova, in Rubzov) Slobodyanyuk, 1991  
*Psyllotylenchus tesquorae* Rubzov & Nikulshin, in Rubzov, 1981  
*Rubzovinema tesquorae* (Rubzov & Nikulshin, in Rubzov) Slobodyanyuk, 1991

No other species.

ETYMOLOGY. Patronym honouring I.A. Rubzov, and *nema* for nematode.

The type species was found parasitizing the flea, *Citellophilus tesquorum*, in the nest litter of *Clitellus pygmaeus* in Novaya Kazanka village, Dzhangalinskii, Ural'skaya, Russia. It leads a free life in the flea's nest, feeding on associated fungi.

#### Remarks

*Rubzovinema* is very similar to other flea-parasitizing Hexatyline (e.g. *Spilotylenchus*, *Psyllotylenchus*, *Kurochkinitylenchus*) which have been assigned to different familial groups due to differences in their life history. As more information on their biology is gathered, a reclassification of these forms will be necessary.

## Genus *inquirendum*

### Genus *Hadrodenus* Mulvey, 1969

(Fig. 142, E–H)

#### Diagnosis

Neotylenchinae. Cuticle finely annulated. Lateral field with six incisures in type species. Cephalic region low, slightly offset by expansion in type species. Stylet distinctly knobbed, 11  $\mu\text{m}$  long in type species. Corpus cylindrical or may have a non-muscular, fusiform swelling posteriorly. Oesophagus joining intestine immediately behind nerve ring; **glands extending over intestine. Vulva at about 77–80% of body length. Postvulval uterine sac well developed**, about one body width long in type species. Ovary outstretched. Female tail elongate-conoid. Male not known.

#### Type species

*Hadrodenus megacondylus* Mulvey, 1969

syn. *Deladenus megacondylus* (Mulvey) Sumenkova, 1975

#### Other species

*Hadrodenus saccatus* (Andrássy, 1954) Mulvey, 1969

syn. *Deladenus saccatus* Andrássy, 1954

ETYMOLOGY. From Greek *hadros* = well developed, and *adenos* = gland.

The type species was found around grass roots in Canada.

#### Remarks

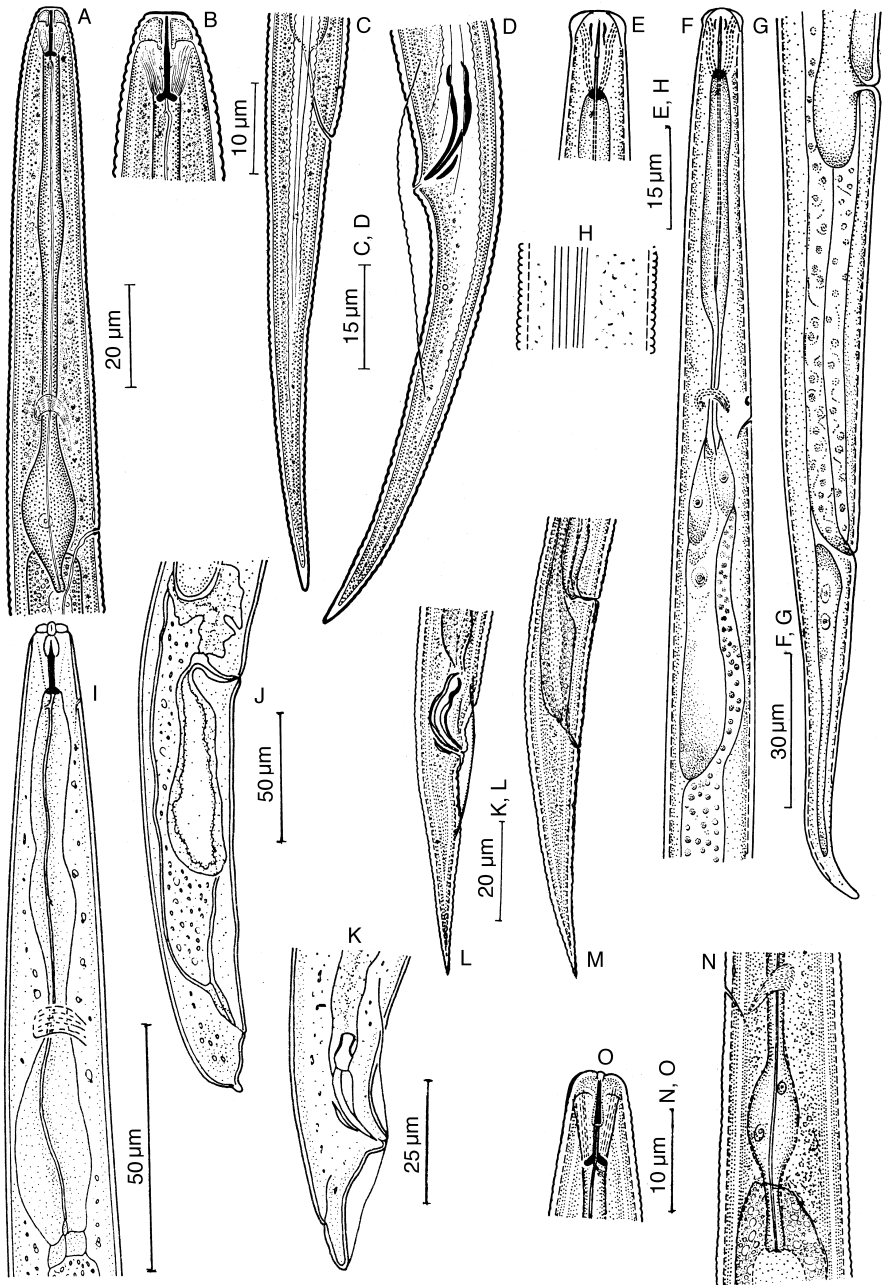
*Hadrodenus* Mulvey, 1969 was assigned to Nothotylenchinae of Anguinidae by Siddiqi (1986). It has been considered as a junior synonym of *Deladenus* by several workers. It is excluded from *Deladenus* mainly because the vulva is not located far posteriorly (vulva at less than two vulval body widths from anus in *Deladenus* spp.) and there is a well-developed postvulval uterine sac. Moreover, insect-parasitic stages of *Hadrodenus* species are not known. It is therefore proposed as *genus inquirendum* under Neotylenchidae.

## Family *Sphaerulariidae* Lubbock, 1861 (Skarbilovich, 1947)

syn. *Sphaerulariaceae* Lubbock, 1861

#### Diagnosis

Sphaerularioidea. **Free-living generation may be present** (not known for type genus). Only adult heterosexual female or its uterium parasitic in insect hosts; male not found in host. **Parasitic female in host haemocoel everts uterus** which normally hypertrophies into a large sac (= uterium) containing oviduct, ovary, eggs and juveniles, leading an independent life. **Free-living forms: Free-living generation present, suspected to be present, or absent.** Partially free-living forms of entomoparasitic generation present in environment. Free-living generation forms as described in diagnosis of the superfamily. **Partially free-living forms:** No marked



**Fig. 142.** A–D. *Paurodontus similis* Siddiqi. E–H. *Hadrodenus megacondylus* Mulvey. I–K. *Neomisticus rhizomorphoides* (Rühm). L–O. *Paurodontella minuta* Husain & Khan. A, F and I. Oesophageal regions of females. B, E and O. Head ends of females. C, G, J and M. Tail ends of females. D, K and L. Tail ends of males. H. Lateral field. N. Basal region of oesophagus. (A–D. After Siddiqi (1961c), courtesy Helminthological Society of Washington. E–H. After Mulvey (1969). I–K. After Rühm (1955). L–O. After Husain & Khan (1968).)

sexual dimorphism in anterior region. **Female:** Stylet well developed, 11–19  $\mu\text{m}$  long, conus with distinct lumen, base plain, tripartite or knobbed. Orifice of dorsal gland just at base of stylet, not detectable in type genus. **Oesophageal glands forming a broad cylindroid or bulboid structure, often with a stem-like extension at base; glands not enlarged**, may form short lobes over intestine. Vulva inconspicuous, small; vagina short. **Postvulval uterine sac present or absent.** Uterus very long in fertilized females, packed with round sperm. Ovary immature. Tail subcylindroid, with a rounded tip. **Male:** Essentially similar to female. Oesophageal glands enclosed in a basal bulb, not extending over anterior end of intestine. Testis outstretched, or reflexed. Spicules cephalated, arcuate, less than 25  $\mu\text{m}$  long. Gubernaculum present. Bursa present, subterminal or enveloping tail tip, or absent (*Tripilus*). Impregnated female invades host.

#### Type subfamily

Sphaerulariinae Lubbock 1861

No other subfamily.

### Subfamily Sphaerulariinae Lubbock, 1861 (Pereira, 1931) syn. Sphaerulariaceae Lubbock, 1861

#### Diagnosis

Sphaerulariidae, with characters of the family.

#### Type genus

*Sphaerularia* Dufour, 1837

#### Other genera

*Prothallonema* Christie, 1938

*Tripilus* Chitwood, 1935

(genera of Paurodontidae may belong here)

#### Key to genera of Sphaerulariinae

1. Entomoparasitic female with partially prolapsed uterus not larger than body;  
male without bursa ..... *Tripilus*  
Entomoparasitic female with completely prolapsed uterus much larger than  
body; male with bursa ..... 2
2. Stylet knobbed; uterium surface smooth; bursa distinct, completely enveloping  
tail; mostly parasites of beetles and their hymenopterous parasitoids  
..... *Prothallonema*  
Stylet not knobbed; uterium surface with numerous large rounded elevations;  
bursa indistinct, subterminal; mostly parasites of bumble bee queens  
..... *Sphaerularia*

## Genus *Sphaerularia* Dufour, 1837

(Figs 143; 144)

### Diagnosis

Sphaerulariinae. **Entomoparasitic forms:** **Female:** Upon entering the insect haemocoel, fertilized female everts its uterus, oviduct and ovary through the vulva. **The uterus containing oviduct and ovary becomes hypertrophied, forms egg-producing sac (= uterium) leading an independent life**, the female becomes an inconspicuous non-functional, wrinkled appendage to it. **Uterium:** sausage-shaped, 2–20 mm (av. 6–9 mm) long, 1.2–1.5 mm wide; surface with rows of broadly based large rounded elevations (= uterine cell nuclei). Eggs generally deposited in host's haemocoel, those retained hatch inside the uterium; eggs about  $160\ \mu\text{m} \times 110\ \mu\text{m}$ . Two moults occur within the egg. **Third-stage juvenile:** in insect haemocoel and soil. Body 0.9–1.5 mm long, 28–34  $\mu\text{m}$  wide, C-shaped or straight when relaxed; stylet 7–11  $\mu\text{m}$  long; tail 32–59  $\mu\text{m}$  long in type species. Lateral field with up to eight incisures. Cephalic region continuous; amphidial apertures conspicuous, dorso-submedian. A pair of hook-like structures on dorsal lip reported, but this could be exudate from amphids. Two oesophageal glands distinct, forming a short lobe over intestine. Tail conoid, bluntly rounded. **Partially free-living forms:** No complete free-living generation known. **Female:** About 1–2 mm long, slender. Cuticle finely annulated. Cephalic region continuous or slightly constricted, smooth. Stylet slender, about 14–18  $\mu\text{m}$  long, conus with distinct lumen; base smooth without knobs or thickenings, or rarely split into three flanges. Substylet gland orifice not seen. Two oesophageal glands distinct, abutting or slightly overlapping intestine; their orifices far behind stylet, 59–75  $\mu\text{m}$  from anterior end of body in type species. Excretory pore behind nerve ring. Vulva posterior but **at more than two body widths from anus**. **Postvulval uterine sac present**, less than a body width long. Uterus very elongated, with several hundred sperm when impregnated, usually extending to middle of body. **Oviduct very long**. Ovary also long but under-developed, outstretched or reflexed. Rectum and anus distinct. Tail conoid-pointed, in type species 47–68  $\mu\text{m}$  long, with terminal portion irregular in outline. **Male:** Smaller than female but oesophagus poorly developed. Stylet 9–17  $\mu\text{m}$  long, conus, often curved ventrally. **Tail similar to that of female**. **Bursa subterminal**, not conspicuous. Testis reflexed; in young male outstretched. Spicules arcuate, cephalated, 17–23  $\mu\text{m}$  long. Gubernaculum 5–8  $\mu\text{m}$  long in type species.

### Hosts

Hymenoptera: *Bombus*, *Psithyrus*, *Vespa*.

### Type species

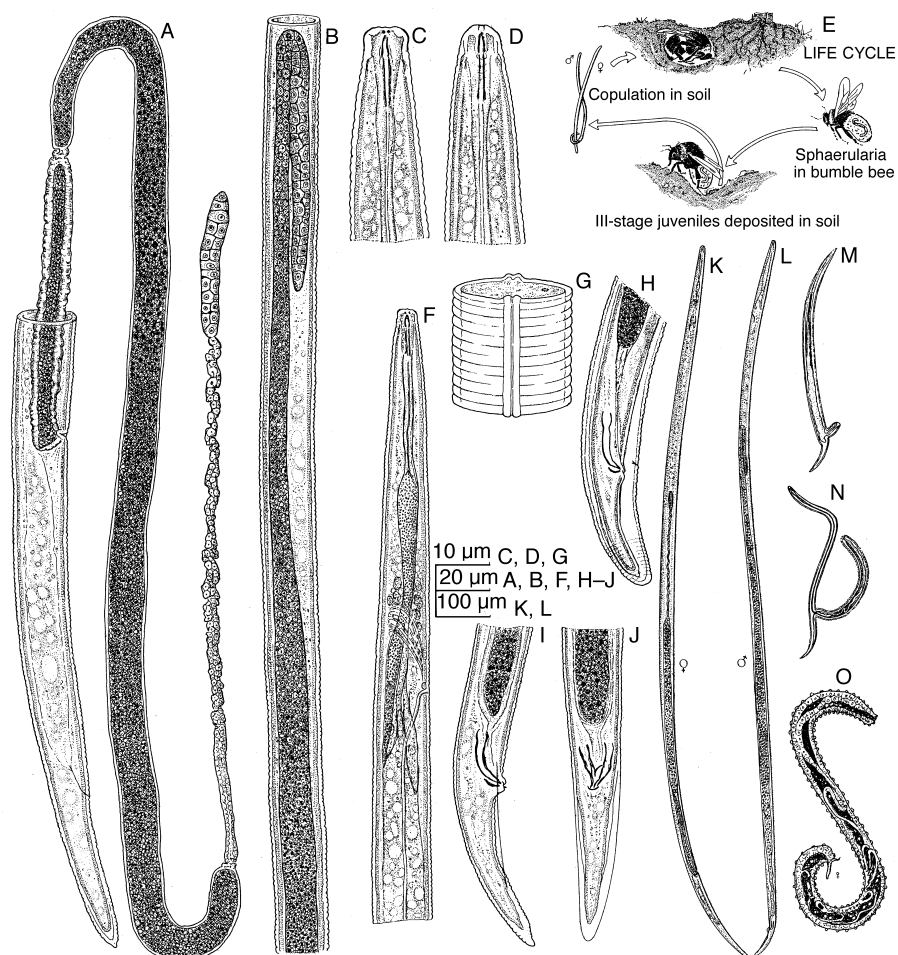
*Sphaerularia bombi* Dufour, 1837

syn. *Tylenchus bombi* (Dufour) Cobb, 1890

No other species.

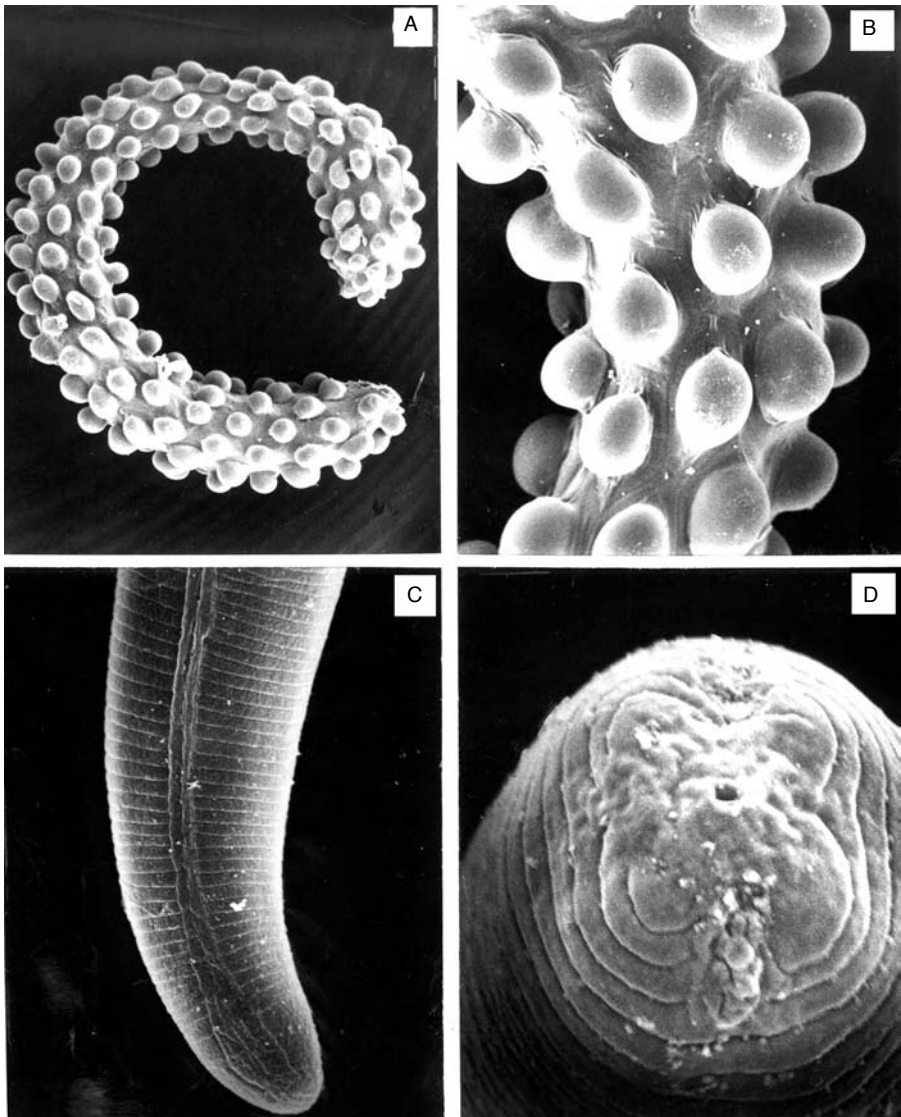
### Remarks

*Sphaerularia bombi* parasitizes queen bumble bees, *Bombus* spp., and the bumble bee nest parasite, *Psithyrus insularis*, in Canada (McCorquodale *et al.*, 1998) and is wide-



**Fig. 143.** *Sphaerularia bombi* Dufour. A. Posterior end and gonoduct of impregnated, preadult entomoparasitic female. B. Testis. C. Head end of preadult female. D. Head end of male. E. Life cycle. F. Anterior end of preadult female. G. Lateral field. H. Tail end of male fourth-stage juvenile. I and J. Tail ends of males. K and L. Female and male, respectively. M and N. Female with everted uterus. O. Uterium with shrivelled female at lower lip. (M–O. After R. Leuckart (1887). Remainder after Siddiqi (1986).)

spread in Europe and North America. Khan (1957) recorded *S. bombi* on *Bombus terricola* Kirby and *B. ternarius* Say in Canada. In Holland, Poinar & Van der Laan (1972) observed queen bumble bees digging in the soil or soil under moss and rotting tree stumps, depositing third-stage juvenile nematodes through their anus. The nematodes moulted for the last time in the soil and became adults in about 2 months. The impregnated females penetrated the new host, probably a hibernating queen. Some nematodes occur in atrophied oviducts and uteri of queens and may



**Fig. 144.** Scanning electron micrographs of *Sphaerularia bombi* Dufour. A and B. Uterium (partly shrunk). C. Tail end of juvenile from haemocoel of a bumble bee. D. *En face* view of juvenile from haemocoel of a bumble bee.

leave the host via its reproductive system. Parasitized queens do not make brood nests, keep on flying for long periods and are generally sterilized and even killed by heavy infection. Most of the eggs of the uterus were found to be laid in the host's haemocoel in 7 days and hatched in 4–7 days. Juveniles developed in the laboratory through two moults to preadults in 4–5 months, female to male ratio being 2:1 (Madel, 1966).



ETYMOLOGY. From Greek *sphaira* = globe, dim. *sphairula* (for the shape of everted uterium).

The type species was described as parasitizing queen bumble bee, *Bombus* sp. in France.

**Genus *Prothallonema* Christie, 1938**

syn. *Stictylus* Thorne, 1941

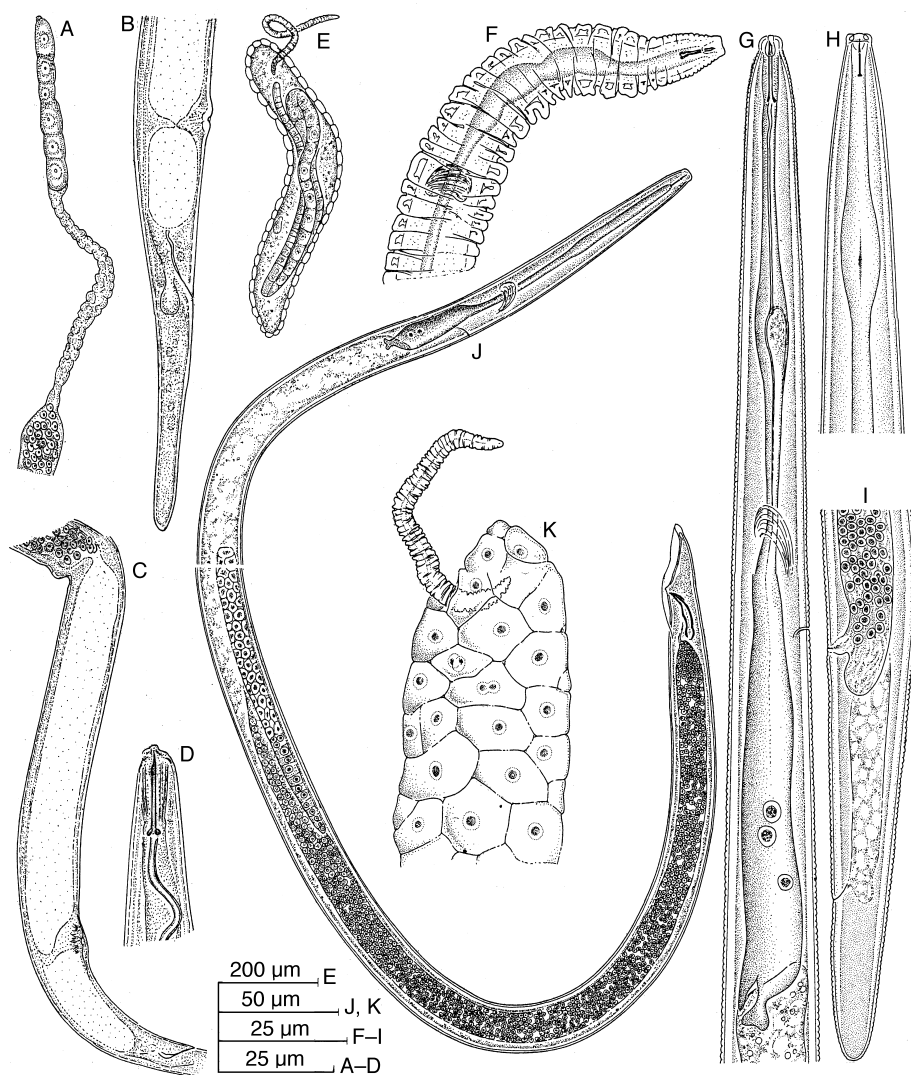
***Sphaerulariopsis* Wachek, 1955**

***Cylindrotylenchus* Yang, 1985**

(Figs 145, A–K; 159, A–K)

**Diagnosis**

Sphaerulariinae. With free-living fungus-feeding generations and a heterosexual generation involving adult female parasitic in insect haemocoel. No complete cycle in insect host. **Entomoparasitic forms** (not known for type species): **Female:** In insect haemocoel, the female everts its uterus to form an egg-producing sac (the uterium) and becomes a wrinkled appendage to it. Cephalic region, stylet and tail similar to that of preadult free-living female. **Uterium:** 0.8–1 mm and 3.2–3.7 mm long in *P. hastata* and *P. stammeri*, respectively; **with smooth surface.** Ovary and oviduct coiled within. Eggs continuously produced and laid in the haemolymph. In *P. stammeri*, early-stage juveniles in haemocoel 0.3–0.4 mm long, with knobbed stylet 7–8  $\mu\text{m}$  long and conoid-rounded tail; preadult fourth-stage male and female juveniles about 0.55–0.65 mm long, leave the host via rectum for further development and copulation. **Free-living forms: Mycetophagous generation: Female:** Body about 1.5 mm long (1.38–1.54 mm in type species);  $a < 50$ . Cuticle finely annulated. Lateral field usually with six (rarely four) incisures. Cephalic region low, continuous, smooth; **framework eight-sectored, lateral sectors smaller than submedians.** Stylet slender, about 10  $\mu\text{m}$  or less long; basal knobs asymmetrical, sometimes divergent swellings. **Orifice of dorsal gland just at base of stylet.** Corpus cylindroid or with a fusiform swelling posteriorly. Isthmus short. **Basal bulb large, saccate, with a short terminal stem-like projection,** enclosing oesophageal glands; dorsal gland may slightly extend over intestine. Excretory pore behind nerve ring, duct usually distinct. Intestine with a postrectal blind sac. **Vulva at about 90% of body length** (88–94% in type species). **Postvulval uterine sac present.** Ovary often reflexed due to excessive growth. **Quadricolumella with more than four cells in each row.** Tail cylindroid or subcylindroid, with obtuse terminus which may sometimes bear a peg. **Male:** Essentially similar to mature free-living female, 1.1–1.3 mm long;  $a = 33$ –37 in type species. **Tail conical, completely enveloped by a prominent bursa.** Spicules and gubernaculum typical of the family. **Entomoparasitic generation: Partially free-living female:** Preadult, partially free-living but not capable of feeding on fungi. About 1 mm long (0.96–1.1 mm,  $a = 29$ –40 in type species), occasionally 0.4 mm long. Cuticle finely striated, with lateral fields. Stylet 11–19  $\mu\text{m}$  long, **with prominent knobs;** orifice of dorsal gland closely behind knobs. Oesophageal glands forming a long, broad, cylindroid bulb, with a stem-like extension joining intestine. Excretory pore behind nerve ring. Vulva near anus. Postvulval uterine sac indicated when uterus is distended with sperm. Uterus very long, may



**Fig. 145.** A–D. *Prothallonema dubium* Christie (= *P. intermedium*), paralectotypes, preadult entomoparasitic females. A. Ovary and oviduct. B. postvulval region. C. Vulval region. D. Head end. E–K. *Prothallonema hastatum* (Khan) from the haemocoel of *Dendroctonus monticolus*. E, F and K. Female after formation of the uterus. G and I. Preadult entomoparasitic female. H. Anterior end of juvenile.

extend to middle of body. Impregnated uterus packed with rounded sperm. Oviduct short. Ovary immature with a few oocytes. **Tail subcylindroid, with a broadly rounded terminus.** Impregnated female invades host. **Male:** 0.5–1.3 mm long (1.1–1.3 mm long,  $a = 33\text{--}37$  in type species). Stylet about 10–12 µm long,

**knobbed.** Testis outstretched or reflexed. Spicules cephalated, arcuate, about 15–18  $\mu\text{m}$  long. Gubernaculum present. **Bursa large, prominent, enveloping tail.**

#### Hosts

Coleoptera: *Dendroctonus*, *Ernobius*, *Pissodes*.  
Hymenoptera: *Coeloides*.

#### Type species

Type by original designation:  
\**Prothallonema dubium* Christie, 1938

#### Present status

*Prothallonema intermedium* (Christie, 1938) Siddiqi, 1986 (= senior objective synonym of *P. dubium*, by reason of page priority and better-known species)  
syn. *Hexatylus intermedius* Christie, 1938  
*Iotonchium intermedium* (Christie) Filipjev & Schuurmans Stekhoven, 1941  
*Neotylenchus intermedius* (Christie) Thorne, 1941  
*Stictylus intermedius* (Christie) Geraert, Raski & Choi, 1985  
*Prothallonema dubium* Christie, 1938  
*Howardula dubia* (Christie) Nickle, 1965

#### Other species

\**Prothallonema annamari* (Massey, 1974) Siddiqi, 1986  
syn. *Anguillonema annamari* Massey, 1974  
*Stictylus annamari* (Massey) Geraert, Raski & Choi, 1985  
*P. asymmetricum* (Thorne, 1941) Siddiqi, 1986  
syn. *Stictylus asymmetricus* Thorne, 1941  
*P. dendroctoni* (Massey, 1956) Siddiqi, 1986  
syn. *Sphaerularia dendroctoni* Massey, 1956  
*Sphaerulariopsis dendroctoni* (Massey) Nickle, 1963  
*P. hastatum* (Khan, 1957) Siddiqi, 1986  
syn. *Sphaerularia hastata* Khan, 1957  
*Stictylus hastatus* (Khan) Khan, 1960  
*Sphaerulariopsis hastatus* (Khan) Nickle, 1963  
*P. leperisini* (Massey, 1974) Siddiqi, 1986  
syn. *Anguillonema leperisini* Massey, 1974  
*Stictylus leperisini* (Massey) Geraert, Raski & Choi, 1985  
\**P. macrocellum* (Anderson & Das, 1967) Siddiqi, 1986  
syn. *Stictylus macrocellus* Anderson & Das, 1967  
\**P. mucronatum* (Thorne & Malek, 1968) Siddiqi, 1986  
syn. *Stictylus mucronatus* Thorne & Malek, 1968  
\**P. mycophilum* (Rühm, 1956) Siddiqi, 1986  
syn. *Stictylus mycophilus* Rühm, 1956  
\**P. obtusicaudatum* (Schuurmans Stekhoven in Filipjev & Schuurmans Stekhoven, 1941) Siddiqi, 1986  
syn. *Iotonchium obtusicaudatum* Schuurmans Stekhoven in Filipjev & Schuurmans Stekhoven, 1941  
*Neotylenchus obtusicaudatus* (Schuurmans Stekhoven) Skarbilovich, 1952

- \**P. obtusum* (Thorne, 1941) Siddiqi, 1986  
 syn. *Stictylus obtusus* Thorne, 1941
- P. piceae* (Fuchs, 1929) Siddiqi, 1986  
 syn. *Tylenchus sulphureus piceae* Fuchs, 1929  
*Tylenchus sulphureus sulphureus* Fuchs, 1929 (*vide* Fortuner, 1985)  
*Allantonema sulphureus piceae* (Fuchs) Filipjev, 1934  
*Parasitylenchus sulphureus piceae* (Fuchs) Schneider, 1939  
*Stictylus sulphureus piceae* (Fuchs) Rühm, 1956  
*Sphaerulariopsis piceae* (Fuchs) Nickle, 1967
- \**P. pinguicauda* (Fuchs, 1938) Siddiqi, 1986  
 syn. *Anguillonema pinguicauda* Fuchs, 1938  
*Stictylus pinguicauda* (Fuchs) Geraert, Raski & Choi, 1985
- P. pini* (Fuchs, 1929) Siddiqi, 1986  
 syn. *Tylenchus sulphureus pini* Fuchs, 1929  
*Allantonema sulphureus pini* (Fuchs) Filipjev, 1934  
*Parasitylenchus sulphureus pini* (Fuchs) Schneider, 1939  
*Allantonema pini* (Fuchs) Wacheck, 1955  
*Stictylus pini* (Fuchs) Rühm, 1956  
*Sphaerulariopsis pini* (Fuchs) Nickle, 1963
- P. piniphili* (Fuchs, 1929) Siddiqi, 1986  
 syn. *Tylenchus sulphureus piniphili* Fuchs, 1929  
*Allantonema sulphureus piniphili* (Fuchs) Filipjev, 1934  
*Parasitylenchus sulphureus piniphili* (Fuchs) Schneider, 1939  
*Stictylus piniphili* (Fuchs) Rühm, 1956  
*Sphaerulariopsis piniphili* (Fuchs) Nickle, 1963
- P. pseudobtusum* (Rühm, 1956) Siddiqi, 1986  
 syn. *Stictylus pseudobtusus* Rühm, 1956
- P. stammeri* (Wacheck, 1955) Siddiqi, 1986  
 syn. *Sphaerulariopsis stammeri* Wacheck, 1955  
*Stictylus stammeri* (Wacheck) Rühm, 1956
- P. unguilacauda* (Khan, 1957) Siddiqi, 1986  
 syn. *Sphaerularia unguilacauda* Khan, 1957  
*Stictylus unguilacauda* (Khan) Rühm, 1960
- P. yangae*, nom. nov., comb. nov.  
 syn. *Cylindrotylechus pini* Yang, 1985  
*Prothallonema pini* (Yang, 1985) comb. n., nec *P. pini* (Fuchs, 1929) Siddiqi, 1986

### Species dubiae

- \**Prothallonema arcuatum* (Thorne, 1941) Siddiqi, 1986  
 syn. *Neotylechus arcuatus* Thorne, 1941  
*Nothanguina arcuata* (Thorne) Nickle, 1968
- \**P. consobrinum* (de Man, 1907) Siddiqi, 1986  
 syn. *Tylenchus consobrinus* de Man, 1907  
*Hexatylus consobrinus* (de Man) Goodey, 1932  
*Neotylechus consobrinus* (de Man) Filipjev, 1936  
*Anguillulina consobrina* (de Man) Schneider, 1939

*Iotonchium consobrinum* (de Man) Filipjev & Schuurmans Stekhoven, 1941

*Paurodontus consobrinus* (de Man) Nickle, 1968

\**P. serpens* (Andrássy, 1961) Siddiqi, 1986

syn. *Neotylenchus serpens* Andrássy, 1961

Species marked with an asterisk are based on free-living forms only.

## Notes

*Cylindrotylenchus* Yang, 1985 was proposed by Yang (1985) for *C. pini* Yang, 1985, and placed in the family Nothotylenchidae because of the structure of the oesophagus. The type species is based on free-living entomopathogenic forms (pre-parasitic females and free-living males) isolated from wilted pine trees in China. *Cylindrotylenchus* is proposed here as a junior synonym of *Prothallonema* and its type species is transferred to the genus *Prothallonema* as *P. pini* which name is occupied by *P. pini* (Fuchs, 1929) Siddiqi, 1986, and hence it is given a replacement name, *Prothallonema yangae*, nom. nov., comb. nov.

ETYMOLOGY. From *prothallus* for fungal hyphae (Greek *pro* = before, *thallos* = young shoot), and *nema* = nematode.

*Prothallonema dubium* was found in an agar-slant culture of a fungus *Alternaria citri*, and a nematode, *Hexatylus intermedius*. Both nematodes originated from a decaying citrus fruit taken from a tree in California, USA, and were described as different species. The nematodes remained in culture for a long time until examined by Christie (1938), who found a large number of *H. intermedius* feeding on fungi and only some specimens of *P. dubium* (in fact immature impregnated infective-stage females) which remained in culture without feeding and/or maturing. The males (which fertilized these females) were also present in the culture. There can be no doubt that the nematodes called *P. dubium* were the dimorphic infective females of *H. intermedius*. They were destined to infect an insect host for further development. Since *H. intermedius* is a better-known species name and with more information, and has page priority, and since *Prothallonema* is distinct from *Hexatylus*, the correct name of the species is *Prothallonema intermedium* (Christie, 1938) Siddiqi, 1986.

Unfortunately, the adult parasitic female and insect host of *P. intermedium* are not known. This situation is the same as with all the members of the family Paurodontidae. However, my study of *P. hastatum* infective female and adult female with everted uterus, from the insect host, affords convincing evidence that *Sphaerulariopsis* and *Stictylus* (note that *Hexatylus intermedius* has been transferred to *Stictylus* by Geraert et al., 1985) are junior synonyms of *Prothallonema*.

*Prothallonema* is close to *Sphaerularia*, from which it differs in having a smaller and smoother uterus, a knobbed stylet, a larger bursa enclosing the tail terminus and in having a different host range.

*Prothallonema hastatum* parasitizes mountain pine beetle (*Dendroctonus monticolae* Hopk.), Douglas-fir beetle (*D. pseudotsugae* Hopk.) and cocoons of their hymenopterous parasite, *Coeloides dendroctoni* Cush., in Canada. All the juveniles leave the host for further development and copulation; the final moult occurs in free life (Khan, 1957). *Prothallonema stammeri* was found parasitizing *Ernobius abietis* Fabricius in Germany. The juveniles leave the host via the rectum after two moults

in free life. The male dies after copulation and the female penetrates the host's larva. The uterus begins to evaginate and, by the time the larva develops to the imago, it has become a large sac, in which the ovary is coiled and egg production starts (Wachek, 1955). *Prothallonema annamari* and *P. leperisini* were found in the USA, associated with *Dendroctonus frontalis* and *Leperisinus aculeatus*, respectively.

### **Genus *Tripilus* Chitwood, 1935**

**syn. *Asconema* Leuckart, 1886**

(= homonym of *Asconema* Schmidt, 1880)

***Atractonema* Leuckart, 1886 (Leuckart, 1887)**

(= homonym of *Atractonema* Stein, 1878)

***Proattractonema* Bovien, 1944**

(Fig. 146, A–G)

### **Diagnosis**

Sphaerulariinae. **Entomoparasitic female:** Obese, partly mobile, small (0.6–0.9 mm long, 0.25–0.28 mm wide), fusiform with pointed ends representing head and tail cones. Stylet present in normal position. Oesophagus degenerate. Intestine transformed into a 'solid' organ of food storage ('speicherorgan') with large cells that become syncytial in older specimens; anus visible but non-functional. Ovary and oviduct slender, coiled. **Uterus thick-walled, partially prolapsed**, may become as large as body or appear as a large cluster of cells protruding through the vulva, forming a flower-like pattern; cell cluster may be partially withdrawn in older females. Oviparous; eggs are ejected through a narrow uterine lumen surrounded by prolapsed cells. **Partially free-living forms: Female:** Slender, about 0.4 mm long, 16–20 µm wide. **Stylet well developed, with tripartite base**, about 14 µm long. **The two subventral oesophageal glands reach near to midbody.** Vulva posterior, small. Short postvulval uterine sac present. Ovary rudimentary. Tail conoid-pointed. **Male:** Slightly shorter than free-living female. Stylet weakly developed, not knobbed or tripartite. Oesophagus degenerate. Excretory pore behind nerve ring. Tail conoid-pointed. Testis outstretched. Spicules straight to arcuate, cephalated, about 11 µm long. Gubernaculum small. Bursa absent.

### **Host**

Diptera: *Bradysia*, *Cecidomyia* (or *Dasyneura*), *Sciar*a.

### **Type species**

*Tripilus gibbosus* (Leuckart, 1886) Chitwood, 1935

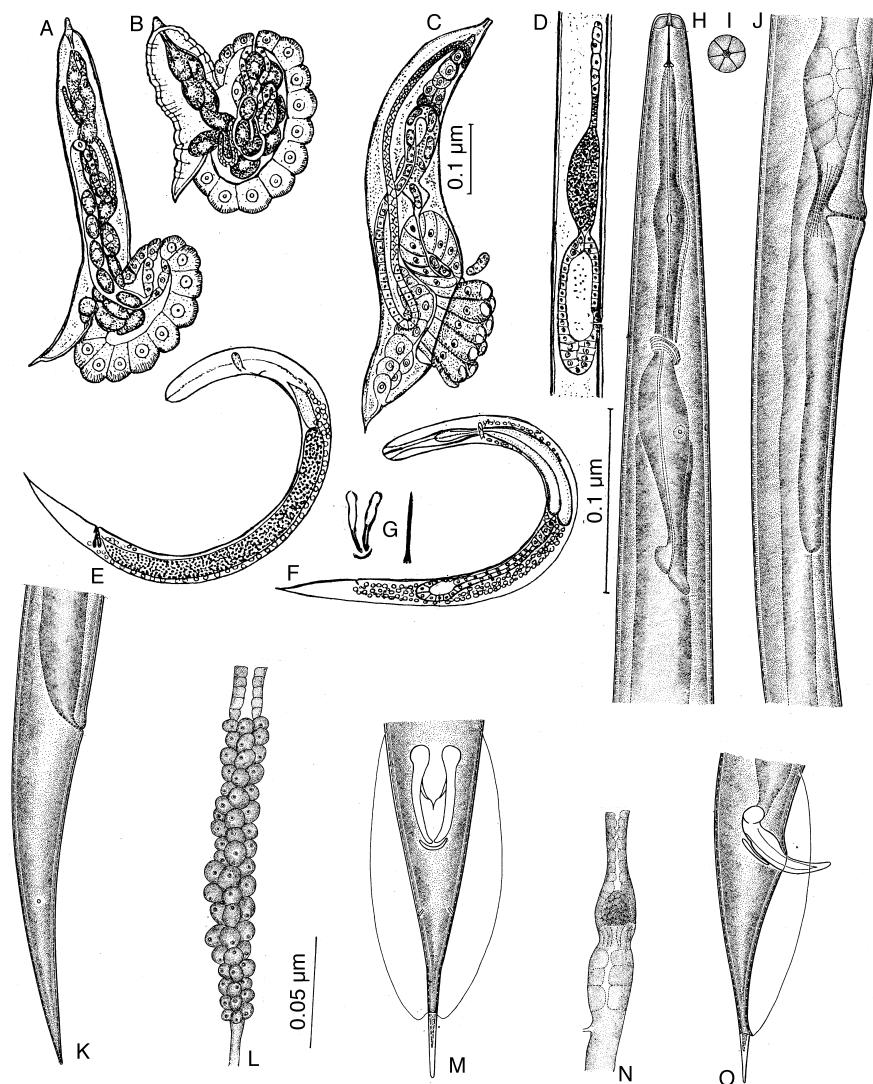
syn. *Asconema gibbosum* Leuckart, 1886

*Atractonema gibbosum* (Leuckart) Leuckart, 1887

### **Other species**

*Tripilus sciarae* (Bovien, 1944) Wachek, 1955

syn. *Proattractonema sciarae* Bovien, 1944



**Fig. 146.** A and B. *Tripilus gibbosus* (Leuckart), female with partially everted uterus. C–G. *Tripilus sciarae* (Bovien). C. Female with partially everted uterus. D and F. Preadult infective female. E. Free-living male. G. Spicule, gubernaculum and female stylet. H–O. *Misticius mustus* Massey. H. Oesophagus. I. En face view of female. J. Vulval region. K. Tail end of female. L. Crustaformeria. M and O. Tail ends of male. N. Spermatheca region (A and B. After R. Leuckart (1887). C–G. After Bovien, 1944. H–O. After Massey (1967).)

#### Remark

Chitwood (1935) proposed the replacement generic name *Tripilus* for *Asconema* Leuckart, 1886 (type species *A. gibbosus* Leuckart, 1886) which was a homonym of *Asconema* Schmidt, 1880 (sponges) and for *Atractonema* Leuckart, 1887 (proposed

by Leuckart (1887) as a replacement name for *Asconema* Leuckart, 1886), which was found to be occupied by *Atractonema* Stein, 1878 (protozoan).

ETYMOLOGY. From the Latin *tri* = three, and *pes* = leg (for tripartite stylet base).

The type species was found parasitizing larvae and imagines of gall-midges, *Cecidomyia pini* De Geer, in Germany.

## Family Paurodontidae Thorne, 1941 (Massey, 1967) (= familia dubia)

### Diagnosis

Hexatylna. Fungus-feeding generation present; entomoparasitic forms not known, most probably exist. Small to large-sized (0.3–2.9 mm). No sexual dimorphism in anterior region. Cephalic region low, rounded or flattened, often distinctly striated; framework six- or eight-sectored, lightly to moderately sclerotized. Stylet under 20 µm long, often knobbed. Oesophagus divisible into corpus, isthmus and basal bulb. Corpus cylindrical or with a non-muscular fusiform swelling at base. **Basal bulb with a stem-like extension** penetrating into intestine. Vulva posterior. Ovary outstretched; tip may be reflexed. Bursa adanal to enveloping tail. Spicules cephalated. Gubernaculum simple. Tails variable in shape, generally similar between sexes.

### Type subfamily

Paurodontinae Thorne, 1941

No other subfamily.

### Note

Most probably, this family is a junior synonym of Sphaerulariidae since the type genus and other genera included in it are morphologically similar and are suspected of having similar life cycles to members of the latter group.

## Subfamily Paurodontinae Thorne, 1941 syn. Misticiinae Massey, 1967

### Diagnosis

Paurodontidae. With characters of the family.

### Type genus

*Paurodontus* Thorne, 1941

### Other genera

*Bealius* Massey & Hinds, 1970

*Luella* Massey, 1974

*Misticius* Massey, 1967

*Neomisticius* Siddiqi, 1986

*Paurodontella* Husain & Khan, 1968

*Paurodontoides* Jairajpuri & Siddiqi, 1969



**Key to genera of Paurodontinae**

1. Stylet with basal knobs ..... 2  
    Stylet without basal knobs ..... *Luella*
2. Excretory pore near stylet base ..... 3  
    Excretory pore near nerve ring ..... 4
3. Body extremely slender ( $a > 60$ ); female tail elongate-conoid; male tail not completely enveloped by a bursa ..... *Misticus*  
    Body not extremely slender ( $a < 40$ ); female tail short, subcylindrical; male tail completely enveloped by a bursa ..... *Neomisticus*
4. Postvulval uterine sac prominent ..... 5  
    Postvulval uterine sac rudimentary, or absent ..... 6
5. Vulva at less than two body widths from anus; bursa terminal ..... *Paurodontoides*  
    Vulva at more than two body widths from anus; bursa adanal ..... *Paurodontus*
6. Vulval lips modified, anterior lip extending over vulva; bursa enclosing tail tip ..... *Bealius*  
    Vulval lips not modified; bursa not enclosing tail tip ..... *Paurodontella*

**Genus *Paurodontus* Thorne, 1941**

(Fig. 142, A–D)

**Diagnosis**

Paurodontinae. Body straight to ventrally arcuate, under 1.5 mm long. Cuticle finely but distinctly striated. Lateral fields distinct, each with four or six incisures. Cephalic region continuous; framework lightly sclerotized; six sectors of equal size. Stylet under 15  $\mu\text{m}$  long; knobs rounded, symmetrical. Orifice of dorsal oesophageal gland close to stylet base. Excretory pore generally at or near base of oesophagus. Deirids at level of excretory pore. Corpus generally with a posterior fusiform swelling. **Basal bulb somewhat spindle-shaped**, with a short tubular basal projection, in type species enclosed in a peculiar chamber said to be formed by the extended walls of the intestine, but apparently resulting from the detachment of the basal bulb from the protoplasmic mass surrounding it. Vulva at 71–84% (76% in type species) of body length, at more than two body widths from anus; lips slightly prominent, not modified. **Postvulval uterine sac prominent**, about one body width long in type species. Ovary anteriorly outstretched. Tails elongate-conoid to filiform, similar in sexes. **Bursa adanal**, crenate. Testis outstretched. Spicules 18–26  $\mu\text{m}$  long. Gubernaculum simple. Associates of roots and soil fungi.

**Type species***Paurodontus gracilis* Thorne, 1949**Other species***Paurodontus affinis* Gagarin, 1999*P. bajrai* Khan, Mathur, Nand & Prasad, 1968*P. brassicae* Das & Shivaswamy, 1980

*P. chawdhuri* Husain & Khan, 1965

*P. indicus* Khan & Nanjappa, 1972

*P. neosimilis* Khan & Basir, 1964

*P. saxeni* Husain & Khan, 1965

*P. similis* Siddiqi, 1961

ETYMOLOGY. From Greek *pauros* = brief, and *odous* (*idion*, diminutive) = tooth (for spear).

The type species was found around roots of cotton in Georgia, USA. *Paurodontus similis* was collected from around roots of *Brassica oleraceae* L. in India. *Paurodontus* spp. are fungus feeders in free life, and may have an insect-parasitic cycle. This was indicated by a species I found on fungi in Luton, England, which is similar to *Paurodontus* spp. except for reduced stylet knobs, and has sphaerularioid pre-parasitic females (see Fig. 159, A–K).

### Genus *Misticus* Massey, 1967

(Fig. 146, H–O)

#### Diagnosis

Paurodontinae. Body 1.5 mm or longer (female 2.4–2.9 mm, male 1.5–2.4 mm in type species), **extremely slender** ( $a > 60$ ). Cuticle finely striated. Lateral incisures absent. Cephalic region low, smooth, almost continuous with body; framework lightly sclerotized. Stylet moderately stout, with prominent symmetrical basal knobs, 12–14  $\mu\text{m}$  long in type species. Postcorpus spindle-shaped, non-muscular, non-valvate but slight cuticular thickening in centre in type species. Basal bulb with a long stem-like extension opening subventrally into intestine, overlapped by intestine for up to two body widths. **Excretory pore far forward near stylet base**. Hemizonid near nerve ring. Vulva posterior, at 87–91% of body length and postvulval uterine sac over two body widths long in type species. Prodelphic, ovary outstretched, with tip occasionally reflexed. Quadricolumella with more than 12 cells in each row. Spicules cephalated, stout, apparently fused distally. Gubernaculum trough-shaped. **Tails elongate-conoid**, over four anal body widths long, ending in a minutely rounded tip. Bursa large, flap-like, **covering about three-fourths of tail**, terminally notched. Associates of insects.

#### Type species

*Misticus mustus* Massey, 1967

No other species.

ETYMOLOGY. From Latin *misticus* = mongrel, mixed race.

The type species was found in the galleries of the beetle *Dendroctonus pseudotsugae* Hopk. in Douglas fir, *Pseudotsuga menzeisii* var. *glauca* (Beissn.), in New Mexico, USA.

**Genus *Neomisticius* Siddiqi, 1986**

(Fig. 142, I–K)

**Diagnosis**

Paurodontinae. Body about 1–2 mm long;  $a = 30$ –35 in type species. Cephalic region low, smooth, rounded. Stylet about 12  $\mu\text{m}$  long, with distinct rounded knobs. Orifice of dorsal oesophageal gland close to stylet base. Corpus cylindroid, with a slight non-muscular swelling at base; isthmus short; basal bulb large, pyriform, stem-like basal extension apparently short in type species. **Excretory pore opposite or near base of stylet.** Vulva far posterior, at 91–93% in type species. Vagina almost at right angles to body axis. Postvulval uterine sac large, about one and a half body widths long, extending to more than half vulva–anus distance in type species. Ovary anteriorly outstretched. **Female tail short, subcylindrical, with a knob-like terminal process** in type species. Male tail conoid-rounded. Spicules broad anteriorly. Gubernaculum simple. **Bursa large, enveloping tail.**

**Type species**

*Neomisticius rhizomorphoides* (Rühm, 1955) Siddiqi, 1986

syn. *Anguillonema rhizomorphoides* Rühm, 1955

No other species.

**Remark**

*Neomisticius* Siddiqi, 1986 differs from *Misticius* in having a different tail shape and bursa enveloping entire tail.

ETYMOLOGY. From *neos* = young, new, and *Misticius*.

**Genus *Paurodontella* Husain & Khan, 1968**

syn. *Neopaurodontus* Tikyani & Khera, 1968

(Fig. 142, L–O)

**Diagnosis**

Paurodontinae. Body short and robust ( $L = 0.3$ –0.4 mm in type species;  $a = 30$ ). Lateral fields distinct, each with four, six or seven incisures. Cephalic region continuous; lateral sectors narrower than submedians. Stylet 8–10  $\mu\text{m}$  long in type species; basal knobs symmetrical or nearly so, rounded, flattened posteriorly. Orifice of dorsal oesophageal gland just behind stylet base. Corpus cylindroid, slightly swollen posteriorly; isthmus long, slender; **basal bulb with long stem-like extension**, projecting into the intestine. Excretory pore opposite or behind nerve ring. Vulva–anus distance about one tail length or less; vulval lips not prominent or modified. Vagina less than half body width long, usually at right angles to body axis. **Postvulval uterine sac absent**, uterus often with an offset diverticulum. Ovary anteriorly outstretched, with oocytes mostly in one row and reaching oesophagus. Tails of both sexes similar, conoid-pointed, up to four anal body widths long. Bursa adanal. Spicules moderately robust, cephalated, 15–20  $\mu\text{m}$  long in type species. Gubernaculum simple. Free-living in soil around roots, may be fungal feeders.

## Type species

*Paurodontella minuta* Husain & Khan, 1968

syn. *Paurodontus minutus* (Husain & Khan) Fortuner & Raski, 1987

## Other species

*Paurodontella aberrans* (Nandakumar & Khera, 1969) Sumenkova, 1975

syn. *Paurodontus aberrans* Nandakumar & Khera, 1969

*P. apitica* (Thorne, 1941) Husain & Khan, 1968

syn. *Paurodontus apiticus* Thorne, 1941

*P. asymmetrica* (Tikyani & Khera, 1968) Sumenkova, 1975

syn. *Neopaurodontus asymmetricus* Tikyani & Khera, 1968

*P. auriculata* Anderson, 1985

syn. *Paurodontus auriculatus* (Anderson) Fortuner & Raski, 1987

*P. densa* (Thorne, 1941) Husain & Khan, 1968

syn. *Paurodontus densus* Thorne, 1941

*P. niger* (Thorne, 1941) Husain & Khan, 1968

syn. *Paurodontus niger* Thorne, 1941

*P. sohailai* Maqbool, 1982

syn. *Paurodontus sohailai* (Maqbool) Fortuner & Raski, 1987

The type species was found around roots of *Allium cepa* L. in India. *Paurodontella apitica*, *P. densa* and *P. niger* were found in the USA around roots of *Larrea tridentata*, date palm and shadscale, respectively.

**Genus *Paurodontoides* Jairajpuri & Siddiqi, 1969**

(Fig. 139, E–K)

## Diagnosis

Paurodontinae. Small-sized (0.45–0.91 mm long in type species). Cuticle finely striated; lateral fields narrow, each with four incisures. Cephalic region low, continuous, smoothly rounded; **framework eight-sectored**; lateral sectors reduced. Stylet small (9–10  $\mu\text{m}$  long in type species); knobs distinct in type species, **asymmetrical, sub-ventrals notched**; orifice of dorsal oesophageal gland 1  $\mu\text{m}$  from base of stylet. Corpus elongate-fusiform, non-muscular. Isthmus short. Basal bulb elongate pyriform, with a **short stem-like basal extension opening into intestine slightly ventrally**. Excretory pore behind nerve ring. Deirids absent. Vulva near anus (at less than two body widths), lips symmetrical, slightly raised. **Postvulval uterine sac present**. Ovary outstretched, oocytes in one row. Spermatheca axial, with moderately large sperm; sperm may occur in postuterine sac. One egg in uterus at a time. Eggs 48–59  $\times$  17–19  $\mu\text{m}$  in type species. Rectum distinct, anus visible but may be obscure in fixed specimens. Tail shape differs according to sex: elongate-filiform in female, conoid in male. Spicule cephalated, about 20  $\mu\text{m}$  long. Gubernaculum simple. Testis outstretched, occasionally reflexed. **Bursa completely enveloping tail**. Fungal feeders, found around plant roots.

## Type species

- Paurodontoides linfordi* (Hechler, 1962) Jairajpuri & Siddiqi, 1969  
syn. *Neotylenchus linfordi* Hechler, 1962  
*Paurodontus linfordi* (Hechler) Nickle, 1968  
*Prothallonema linfordi* (Hechler) Ebsary, 1991

## Other species

- Paurodontoides latus* (Thorne, 1935) Siddiqi, 1986  
syn. *Neotylenchus latus* Thorne, 1935  
*Iotonchium latum* (Thorne) Filipjev & Schuurmans Stekhoven, 1941

The type species was found in soil around the roots of *Clematis* sp. in Illinois, USA. It was easily cultured on fungi; single female progenies reached 40,000–70,000 nematodes in 30 days (Hechler, 1962).

**Genus *Luella* Massey, 1974**

(Fig. 147, A–E)

## Diagnosis

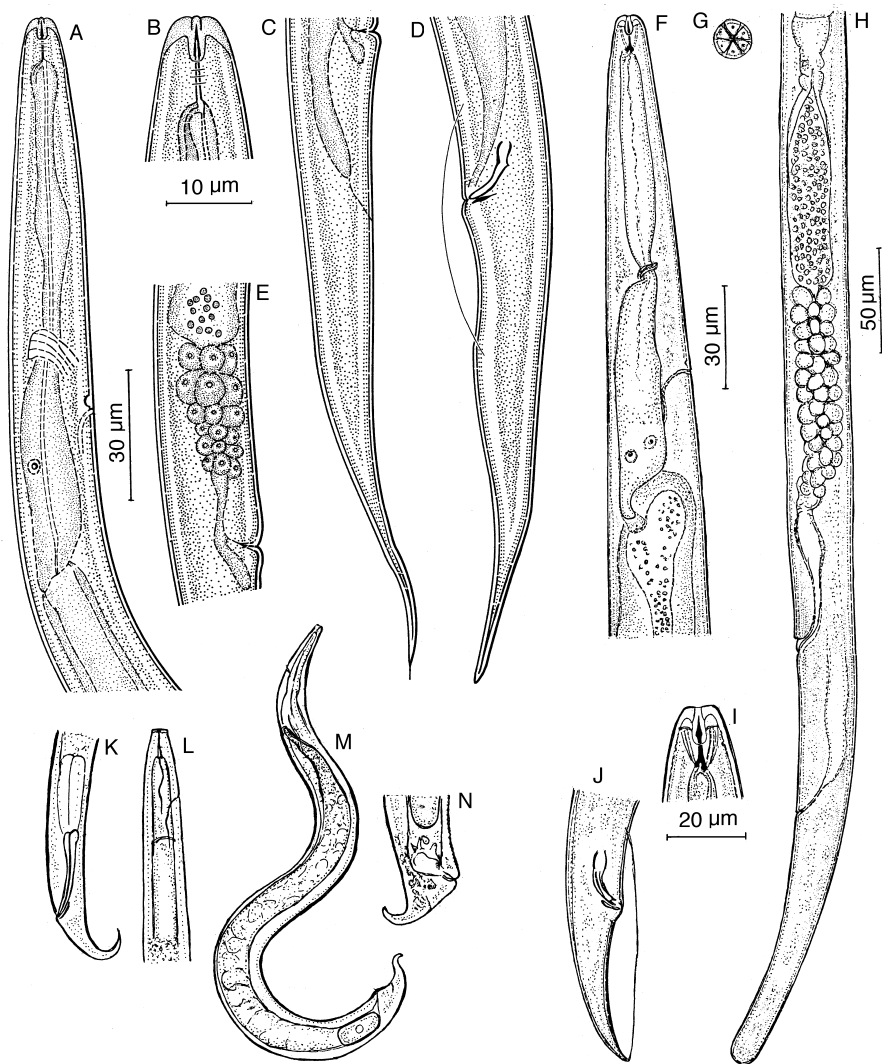
Paurodontinae. Under 1 mm long. **Lateral fields lacking incisures.** Cephalic region continuous, smooth. Stylet slender, **lacking basal knobs or swellings**, 8  $\mu$ m long in type species. Orifice of dorsal gland at stylet base. Postcorpus fusiform, non-muscular. Basal bulb large, offset from intestine, basal region may be lobed dorsally. Excretory pore just behind nerve ring. Vulva less than two body widths from anus, at 80% of body length in type species. **Postvulval uterine sac rudimentary.** Quadricolumella short, one to two body widths long. Ovary reflexed at tip. **Tails in both sexes similar, elongate-conoid to a filiform terminus.** **Bursa adanal**, covering about one-third of tail in type species. Spicules small (about one anal body width long), ventrally arcuate, cephalated. Gubernaculum small. Insect associate, possibly fungal feeder in free life.

## Type species

- Luella luculenta* Massey, 1974  
No other species.

ETYMOLOGY. Patronym honouring Mrs Luella Kramer of Rocky Mountain Forest and Range Experiment Station, Albuquerque, New Mexico, USA.

The type species was found associated with *Ips pini* (a bark beetle) in red pine in Caroline County, New York, USA. Possibly the species is based on a free-living stage of an insect parasite.



**Fig. 147.** A–E. *Luella luculenta* Massey. A. Oesophagus. B. Head end. C and D. Tail ends of female and male, respectively. E. Vulval region. F–J. *Bealius bisulcus* Massey & Hinds. F. Oesophagus. G. *En face* view. H. Posterior region of female. I. Head end. J. Tail end of male. K–N. *Anguillonema poligraphi* Fuchs. K and L. Posterior and anterior regions of male, respectively. M. Gravid female. N. Tail end of gravid female. (Modified: A–E. After Massey (1974). F–J. After Massey & Hinds (1970). K–N. After Fuchs (1938).)

**Genus *Bealius* Massey & Hinds, 1970**

(Fig. 147, F–J)

**Diagnosis**

Paurodontinae. Body 0.9–1.5 mm long;  $a = 31\text{--}46$  in type species. **Lateral fields absent.** Cephalic region broadly rounded; with **six equal-sized lip sectors**. Stylet moderately robust, 11  $\mu\text{m}$  long in type species, with asymmetrical flange-like knobs, of which **subventrals are much larger than the dorsal**; orifice of dorsal oesophageal gland between knobs. Corpus swollen; isthmus very short; basal bulb large, saccate; stem-like extension short, **opening into intestine dorsally**. Excretory pore behind nerve ring, opposite basal bulb and just behind hemizonid in type species; excretory duct sclerotized. Vulva flush with body surface; **anterior lip thick, sclerotized, extending over vulva**. Vulva–anus distance less than tail length in type species. Vagina anteriorly directed. Postvulval uterine sac absent. Quadricolumella with eight or more cells in each row. Spermatheca elongate, axial. Ovary usually with two flexures and reaching oesophagus in type species. Tails long, dissimilar between sexes. Female tail club-like with broadly rounded terminus, about four anal body widths long in type species; male tail conical, arcuate, completely enveloped by a well-developed bursa. Spicules anteriorly expanded and cephalated, **conspicuously bifid at tip**. Gubernaculum simple.

**Type species***Bealius bisulcus* Massey & Hinds, 1970syn. *Stictylus bisulcus* (Massey & Hinds) Sumenkova, 1975*Stictylus bisulcus* (Massey & Hinds) Geraert, Raski & Choi, 1985*Prothallonema bisulcus* (Massey & Hinds) Ebsary, 1991**Other species***Bealius pissodi* Massey, 1971syn. *Stictylus pissodi* (Massey) Geraert, Raski & Choi, 1985*Prothallonema pissodi* (Massey) Ebsary, 1991**Remarks**

*Bealius* was synonymized to *Stictylus* (now *Prothallonema*) by Geraert *et al.* (1985) but was reinstated by Siddiqi (1986) because it differed from the free-living stages of *Prothallonema* in having six equal-sized lip sectors and anterior vulval lip being sclerotized and extending over the vulva. *Bealius*, like other members of the Paurontidae, very probably has an adult female of a parasitic generation in the insect haemocoel.

ETYMOLOGY. Patronym honouring J.A. Beal, ex-Director, US Forest Insect Research.

The type species occurred in necrotic canker bark tissues of aspen (*Populus tremuloides*) caused by the fungi *Cenangium* and *Ceratocystis*.

## Family Allantonematidae Pereira, 1931 (Chitwood & Chitwood, 1937) syn. Contortylenchidae Rühm, 1956

### Diagnosis

Sphaerularioidea. **No free-living generation known.** Single heterosexual generation cycle (hermaphrodites in *Anandranema*), with adult female parasitic in insect or mite haemocoel. **Only one type of adult, i.e. heterosexual female present in host** (males and secondary females may occur within maternal body in *Scatonema*). Entomoparasitic female obese, round, oval, spindle-shaped, or elongate sac-like, ventrally or dorsally curved, its body cavity mostly filled with reproductive organs; vulva may be cleft-like (*Contortylenchus*); **uterus not everted. Partially free-living forms:** With or without sexual dimorphism in anterior region. **Female:** Preadult with immature ovary and generally within juvenile cuticle. Stylet about 15 µm or less long, with or without knobs. **Oesophageal glands elongated, lobe-like, subventral glands extending past the dorsal one.** Vulva inconspicuous, small. Vagina short. Postvulval uterine sac short or absent. Uterus elongated, distended when packed with sperm which are minute, rounded. Tail conoid to subcylindroid. **Male:** Essentially similar to female but oesophageal glands not enlarged, oesophagus may be degenerate. Testis outstretched, producing minute, rounded sperm. Spicules arcuate, pointed, usually under 25 µm long. Gubernaculum fixed, rarely absent. Bursa present or absent. Impregnated female invades host.

### Type subfamily

Allantonematinae Pereira, 1931

### Other subfamily

Contortylenchinae Rühm, 1956

### Key to subfamilies of Allantonematidae

1. Entomoparasitic female contorted, dorsally curved; vulva deeply cleft  
..... **Contortylenchinae**
- Entomoparasitic female not contorted, usually not dorsally curved; vulva not  
deeply cleft ..... **Allantonematinae**

### Subfamily Allantonematinae Pereira, 1931

**syn. Allantoneminae Pereira, 1931**  
**(= incorrect original spelling)**

### Diagnosis

Allantonematidae. **No complete generation either in host or in environment.** Entomoparasitic gamogenetic female obese, round, oval, spindle-shaped, or elongate sac-like, ventrally or sometimes dorsally curved but not contorted. Vulva a small transverse slit or indistinct, not deeply cleft. Male with stylet under 15 µm long or lacking stylet in forms with degenerate oesophagus.



## Type genus

*Allantonema* Leuckart, 1884

## Other genera

*Anandranema* Poinar, Ferro, Morales & Tesh, 1993

*Bradynerema* zur Strassen, 1892

*Howardula* Cobb, 1921

*Metaparasitylenchus* Wacheck, 1955

*Neoparasitylenchus* Nickle, 1967

*Parasitylenchoides* Wacheck, 1955

*Pratinema* Chizhov & Sturhan, 1998

*Proparasitylenchus* Wacheck, 1955

*Protylenchus* Wacheck, 1955

*Scatonema* Bovien, 1932

*Sulphuretylenchus* Rühm, 1956

*Thripinema* Siddiqi, 1986

## Key to genera of Allantonematinae

1. Hermaphrodites present, pleomorphic; males absent ..... *Anandranema*  
    Hermaphrodites absent, females not pleomorphic; males present ..... 2
2. Male lacking stylet; oesophagus completely degenerate ..... 3  
    Male with stylet; oesophagus normal or partially degenerate ..... 6
3. Partially free-living female lacking stylet ..... *Bradynerema*  
    Partially free-living female with stylet ..... 4
4. Partially free-living female with stylet distinctly knobbed; parasitic female  
    with juveniles developing inside maternal body ..... *Scatonema*  
    Partially free-living female with stylet not distinctly knobbed; parasitic female  
    with juveniles not developing inside maternal body ..... 5
5. Partially free-living forms generally with clavate tails; parasitic female small,  
    round to oval, can accommodate one or two eggs; parasites of thrips  
    ..... *Thripinema*  
    Partially free-living forms without clavate tails; parasitic female large,  
    generally tuboid, can accommodate a number of eggs or juveniles; not  
    parasites of thrips ..... *Howardula*
6. Parasitic female oval, bean- or C-shaped ..... *Allantonema*  
    Parasitic female elongate-tuboid ..... 7
7. Excretory pore opposite or anterior to nerve ring ..... *Metaparasitylenchus*  
    Excretory pore behind nerve ring ..... 8
8. Bursa absent ..... 9  
    Bursa present ..... 10
9. Parasitic female with outstretched ovary; tail in free-living female and male  
    elongate-filiform, gubernaculum absent ..... *Pratinema*

- Parasitic female with coiled ovary; tail in free-living female and male short-conoid to subcylindroid, gubernaculum present ..... *Protylemchus*
10. Body surface of parasitic female wavy, with constrictions and swellings; stylet sunken into body ..... *Sulphuretylemchus*  
 Body surface of parasitic female neither wavy nor with constrictions and swellings; stylet not sunken into body except occasionally in *Parasitylemchoides* ..... 11
11. Excretory pore in partially free-living forms at 105–125  $\mu\text{m}$  from anterior end ..... *Parasitylemchoides*  
 Excretory pore in partially free-living forms at less than 100  $\mu\text{m}$  from anterior end ..... 12
12. Partially free-living forms with stylet distinctly knobbed; parasites of staphylinid beetles ..... *Proparasitylemchus*  
 Partially free-living forms with stylet poorly knobbed; parasites of bark beetles ..... *Neoparasitylemchus*

#### Note

Distinction between *Metaparasitylemchus*, *Neoparasitylemchus*, *Parasitylemchoides*, *Proparasitylemchus* and *Protylemchus* is difficult. Further studies are required.

#### Genus *Allantonema* Leuckart, 1884

syn. *Tylenchomorphus* Fuchs, 1915

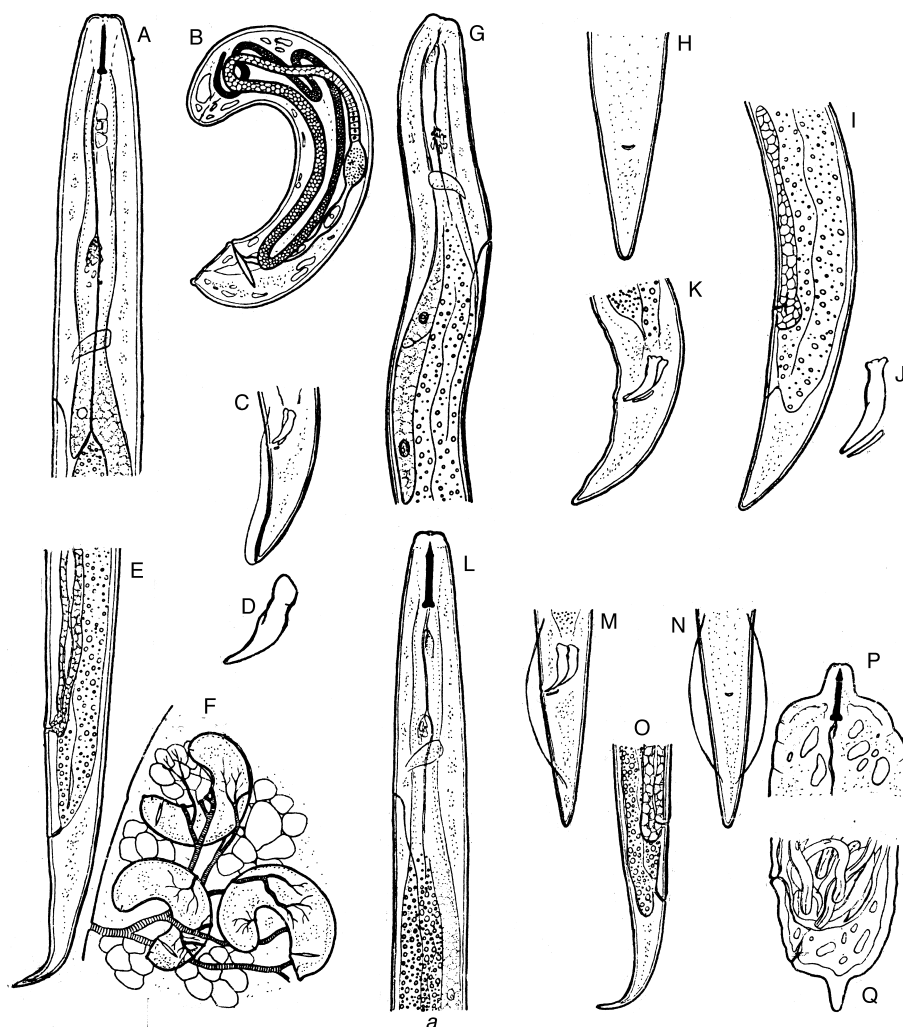
(Fig. 148, A–F)

#### Diagnosis

Allantonematinae. **Entomoparasitic female:** Oval, bean- or C-shaped, generally 1–1.6 mm, or two to four times as long as wide. Stylet retracted from normal position, not functional. Vulva terminal or subterminal. Uterus with numerous synchronous eggs. Ovary often coiled and appearing to float in body, degenerate in older females. Oviparous, rarely ovoviviparous. **Juveniles in host:** Slender, straight upon relaxation. Cuticle smooth (report of longitudinal striae in *A. paramorosum* doubtful, since somatic muscles may easily be mistaken for the striae). Cephalic region usually offset, framework moderately sclerotized. Stylet without basal knobs. Tail tapering to a rounded terminus, two to three anal body widths long. **Partially free-living forms:** **Female:** Body small, slender, dorsally curved (0.36 mm long, 24–25  $\mu\text{m}$  wide in type species). Stylet slender, about 12  $\mu\text{m}$  long, with indistinct basal knobs. Orifice of dorsal gland relatively far behind nerve ring. Vulva far posterior. Postvulval uterine sac absent. Ovary immature, with few oocytes in a row. **Male:** Straight upon relaxation. Stylet present. Testis outstretched. Spicules small, arcuate. Gubernaculum present. Bursa enveloping entire tail.

#### Hosts

Coleoptera: *Crypturgus*, *Geotrupes*, *Hylastes*, *Hyllobius*, *Ochthebius*, *Orthotomicus*, *Philonthus*.



**Fig. 148.** A–F. *Allantonema philonthi* Wacheck. G–K. *Bradynema rigidum* (von Siebold). L–Q. *Proparasitylenchus platystethi* (Wacheck). B, F, P and Q. Mature gametogenetic females from host. A, E, G–I, L and O. Preadult infective females. D and J. Spicules. C, K, M and N. Male tails. F. Three females in body cavity of host in contact with tracheoles to obtain oxygen. (A–Q. Modified after Wacheck, 1955.)

#### Type species

*Allantonema mirabile* Leuckart, 1884

syn. *Tylenchomorphus mirabilis* (Leuckart) Fuchs, 1915

#### Other species

*Allantonema bathycapsulatum* Slankis, 1974

*A. matthesi* Wacheck, 1955

- A. morosum* (Fuchs, 1929) Filipjev, 1934  
 syn. *Tylenchus sulphureus morosus* Fuchs, 1929  
*Parasitylenchus morosus* (Fuchs) Filipjev & Schuurmans Stekhoven, 1941  
*A. orthotomici* Massey, 1974  
*A. paramorosum* Massey, 1974  
*A. philonthi* Wachek, 1955  
*A. silvaticum* von Linstow, 1893

#### Species inquirendae

- Allantonema muscae* Roy & Mukherjee, 1937  
*A. stricklandi* Roy & Mukherjee, 1937  
 (*Allantonema stricklandi* and *A. muscae* appear to be the heterosexual and parthenogenetic female stages, respectively, of a single species of *Heterotylenchus*, as pointed out by Nickle (1967).)

#### Remarks

Juveniles of *A. mirabile* in the haemocoel penetrate the intestine and reach the rectum to be passed out with the faeces. Juveniles taken from the rectum of *Hylobius* readily develop in water, but not those taken from the haemocoel, indicating that the rectal migration is an important aspect of the life cycle; 5–10% of the *Hylobius* population in Denmark was found to be parasitized (Bovien, 1937). Males and preadult females mate in the environment and the latter invade the larva of the beetle by puncturing its cuticle and develop to maturity about the end of the metamorphosis in about 12 days. Leuckart (1887) found juveniles of *A. mirabile* on the elytra of *Hylobius*, which must have escaped via the anus. Wülker's (1923) classical work on *A. mirabile* and *Bradynema strasseni* provided detailed information on the free-living stages and life cycles of these parasites. Wülker (1923) was able to disprove the theory that the parasitic *Allantonema* female might be a proterandrous hermaphrodite. He noticed that numerous spermatogonia and spermatocytes already filled the gonoduct of the male juvenile before even the spicules were formed, and estimated that on the basis of the size of the sperm (each 0.5 µm wide) the female uterus can take 80,000 sperm to be used later to fertilize the numerous eggs produced by the parasitic female. Bovien (1937) showed that in *A. mirabile* the dorsal oesophageal gland opens about one stylet length behind the stylet base.

ETYMOLOGY. From Greek *allas* = sausage, and *nema* = nematode.

The adult females of the type species were found in Germany in the haemocoel of *Hylobius abietis* (L.) wrapped in a special sheath richly supplied with tracheoles.

#### Genus *Howardula* Cobb, 1921

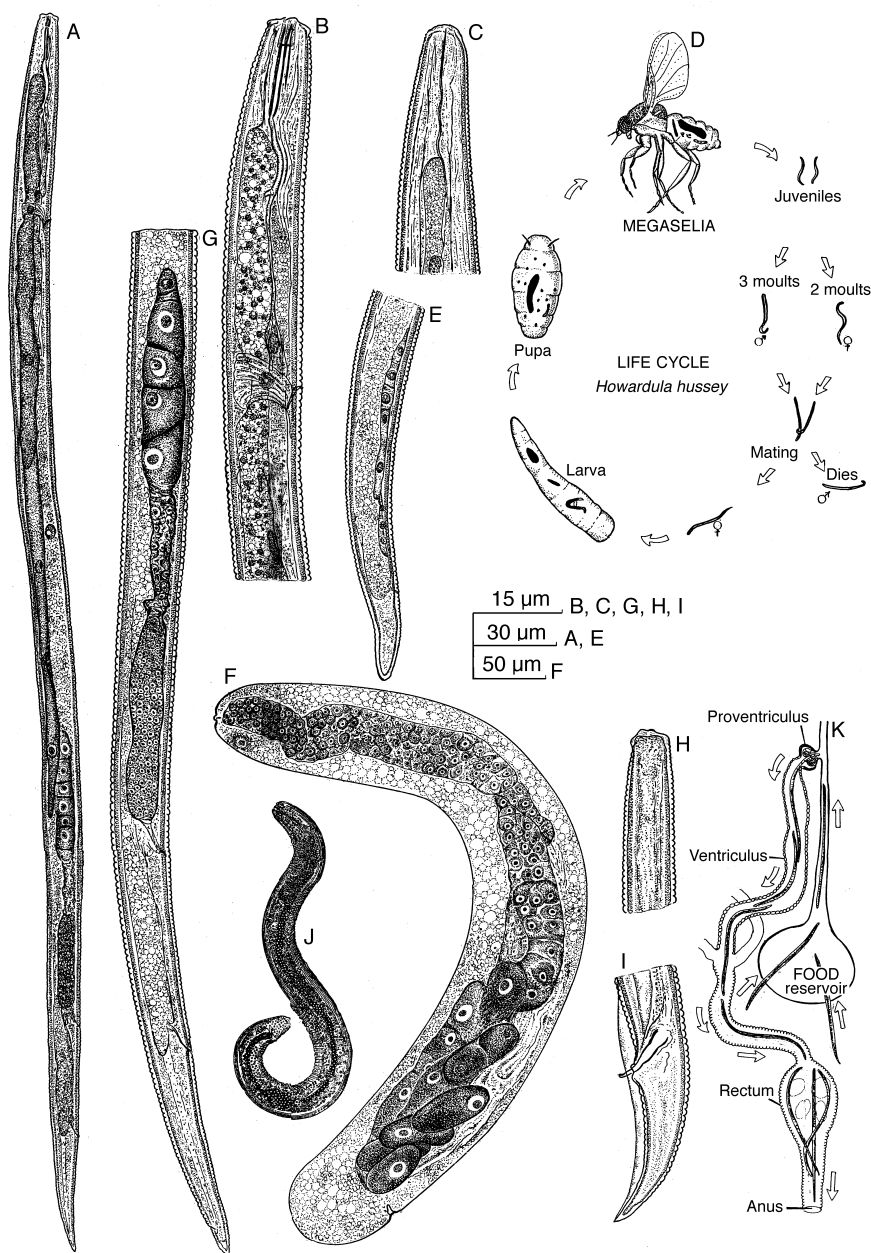
syn. *Acarinocola* Warren, 1941 (= genus dubium)

*Tylenchinema* Goodey, 1930

(Fig. 149)

#### Diagnosis

Allantonematinae. Single generation cycle; **male lacking a stylet**. **Entomoparasitic female:** In body cavity or ovary of insect host. Inert or with slight mobility, obese,



**Fig. 149.** A–I. *Howardula husseyi* Richardson, Hesling & Riding. A. Preadult infective females. B and G. Anterior and posterior ends of preadult infective female. C and E. Anterior and posterior ends of second-stage juvenile. D. Life cycles. F. Entomoparasitic gamogenetic female. H and I. Anterior and posterior ends of free-living male. J. *Howardula benigna* Cobb, entomoparasitic gamogenetic female. K. Diagram showing migration of juveniles of *Howardula oscinellae* through the gut. (J. After Cobb (1921). K. Redrawn after T. Goodey (1931). D. Modified after Richardson *et al.* (1977). Remainder after Siddiqi (1986).)

worm-like, white, not turning yellow or brown. Vulva almost terminal. Oviduct and ovary coiled. Uterus enormous, packed with juveniles in ovoviviparous species and with eggs in oviparous species. Stylet obscure in type species, but seen in others, rod-like without knobs, often sunken in body. **Oesophagus degenerate.** Produces enormous numbers of eggs or juveniles (up to 20,000). Juveniles moult twice or thrice in the host, reach ovary and oviduct to escape through ovipositor or reach gut and escape through anus. **Partially free-living forms:** About 0.5–0.6 mm long. Cuticle finely striated; lateral fields narrow, with incisures. Cephalic region continuous; sclerotization slight or absent. Excretory pore anterior to nerve ring in type species, but may be posterior to it. Female stylet stout, 12–24  $\mu\text{m}$  long, often without basal knobs or thickenings; orifice of dorsal oesophageal gland half to more than one stylet length behind stylet base. Vulva near anus. Ovary rudimentary; uterus acts as a reservoir for sperm. Tail elongate-conoid. **Male without a stylet** or rarely with one which is degenerate. Oesophagus degenerate. Spicules about one anal body width long. Gubernaculum weakly developed or absent. Bursa poorly developed, reaching terminus, or absent. The male dies after inseminating the preadult female. The latter penetrates the host's larva or pupa, remains within and develops through metamorphosis to become adult in the haemocoel of the adult insect.

#### Hosts

Coleoptera: *Apion*, *Carpophilus*, *Colaspis*, *Diabrotica*, *Monolepta*, *Phyllotreta*.  
 Diptera: *Copromyza*, *Oscinella*, *Sepsis*, *Drosophila*.  
 Siphonaptera: *Ctenophthalmus*.  
 Acarina: *Cosmolaelaps*, *Euryparasitus*, *Haemogamasus*, *Parasitus*, *Poecilochirus*.

#### Type species

*Howardula benigna* Cobb, 1921

#### Other species

*Howardula acarinora* Wacheck, 1955  
*H. acris* Remillet & Waerebeke, 1976  
*H. albopunctata* Yatham & Rao, 1980  
*H. aoronymphium* Welch, 1959  
*H. apioni* Poinar, Laumond & Bonifassi, 1980  
*H. belgaumensis* Raj & Reddy, 1989  
*H. colaspidis* Elsey, 1979  
*H. dominicki* Elsey, 1977  
*H. husseyi* Richardson, Hesling & Riding, 1977  
*H. madecassa* Remillet & Waerebeke, 1975  
*H. marginata* Reddy & Rao, 1981 (original spelling *marginatus*)  
*H. mutilata* Devi, Rao & Reddy, 1991 (original spelling *mutilatus*)  
*H. neocosmis* Poinar, Jaenike & Shoemaker, 1998  
*H. oscinellae* (Goodey, 1930) Wacheck, 1955  
     syn. *Tylenchinema oscinellae* Goodey, 1930  
*H. phyllotretae* Oldham, 1933  
*H. saginata* Rajashekar, Rao, Reddy & Reddy, 1995  
*H. truncati* Remillet & Waerebeke, 1975

## Species inquirendae

- Howardula claviger* (Warren, 1941) Wacheck, 1955  
 syn. *Acarinocola claviger* Warren, 1941  
*H. cuneifer* (Warren, 1941) Wacheck, 1955  
 syn. *Acarinocola cuneifer* Warren, 1941  
*H. hirsuta* (Warren, 1941) Wacheck, 1955  
 syn. *Acarinocola hirsutus* Warren, 1941  
*H. prima* Rubzov & Tshumakova in Rubzov, 1981 (species dubia for Poinar *et al.*, 1998)  
*H. stenoloba* Rubzov & Tshumakova in Rubzov, 1981 (species dubia for Poinar *et al.*, 1998)  
*H. terribilis* (Warren, 1941) Wacheck, 1955  
 syn. *Acarinocola terribilis* Warren, 1941

## Remarks

The genus *Acarinocola* Warren, 1941 was considered a junior synonym of *Howardula* by Wacheck (1955), but since its type species is inadequately described and lacks information on male characters and developmental cycle, it should be considered a genus dubium. Its species, *A. claviger*, *A. cuneifer*, *A. hirsuta* and *A. terribilis*, likewise should be regarded as species inquirendae (see Yatham & Rao, 1980). The genus *Prothallonema* Christie, 1938, listed by Nickle (1967) as a synonym of *Howardula*, was considered by Siddiqi (1986) as a valid genus, with which were synonymized the genera *Sphaerulariopsis* and *Stictylus*. A key to species of *Howardula* is given by Zakharenkova (1996).

ETYMOLOGY. Latin diminutive of Howard; feminine gender due to ending -ula.

The type species was found in the USA, parasitizing the body cavity of cucumber-beetles (*Diabrotica* spp.), infesting the two sexes about equally. From a single *D. vittata*, 13,000 juveniles were isolated. The nematode sterilizes the beetle and even kills its adults and grubs (Cobb, 1921).

*Howardula oscinellae* attacks frit-fly, *Oscinella frit* L., throughout England and Wales and occurs in frit-flies in Denmark, Germany and Russia. The parasite causes sterility of both male and female frit-flies by checking the normal development of the gonads. The juveniles from the haemocoel of the adult flies penetrate the thin wall of the food reservoir, a dilation of the oesophagus, and pass down the gut into the rectum to escape (Fig. 149, K) (Goodey, 1931). Welch (1959) reported the exit of juveniles of *H. aoronymphium* through the host's genital or intestinal tract, or both; Cobb (1921) and Oldham (1933) found that the exit of juveniles of *H. benigna* and *H. phyllotretae* was through the female genital systems of cucumber and flea beetles, respectively. A similar exit through the female ovipositor was reported for *H. marginata* parasitic in *Copromyza* flies in India (Reddy & Rao, 1981). *Howardula marginata* is unique in the genus in the oviparous parasitic female having well-developed perivaginal gland cells.

*Howardula apioni*, parasitic in the weevil, *Apion carduorum* Kirby, a pest of artichoke (*Cynara scolymus* L.) in southern France, infects 2–13% of the insect population and develops mostly during the diapause of the adult. The third-stage female

and male juveniles penetrate the host's intestinal wall and emerge from the anus. They are harboured in the stem tissue, where they moult twice and then become adult and mate. The infective female with two unshed cuticles searches out insect larvae, abundant in the plant tissue, to penetrate (Poinar *et al.*, 1980). *Howardula neocosmis* parasitizes *Drosophila acutilabella* in Florida, USA and *D. suboccidentalis* in British Columbia, Canada. The sausage-shaped females inside the adult host fly have numerous eggs, which hatch inside the nematode body. The juveniles leave the nematode body and moult twice within the insect haemocoel before leaving from the insect's genital and digestive tract openings. Once in the environment, the juveniles moult twice to attain the adult stage, mate and then the impregnated females search for and enter a new host (Poinar *et al.*, 1998).

### Genus *Anandranema* Poinar, Ferro, Morales & Tesh, 1993

(Fig. 150)

#### Diagnosis

Allantonematinae. **Entomoparasitic hermaphrodites:** **Pleomorphic** (able to change shape), **from elongate-obese to short and wide, 460–1090  $\mu\text{m}$  long and 48–128  $\mu\text{m}$  wide.** Stylet, excretory pore, oesophagus and anus not visible. Vulva near posterior end, 45–120  $\mu\text{m}$  from tail tip which is broadly rounded. Spermatheca with small (1–2  $\mu\text{m}$  diameter) round sperm present, most conspicuous in younger hermaphrodites. Uterus elongate, with several eggs. Ovary straight or bent once or twice, reaching anterior region in older hermaphrodites. **Oviparous. Infective-stage hermaphrodites:** Body 277–365 (324)  $\mu\text{m}$  long; maximum width 16–23 (19)  $\mu\text{m}$ . Stylet well developed, with distinct basal knobs, 8–11 (10)  $\mu\text{m}$  long; conus set off and thicker than shaft. Orifice of dorsal oesophageal gland just behind stylet base, orifices of subventral glands about two stylet lengths from stylet base. Excretory pore located a little behind nerve ring. Vulva opening inconspicuous. Tail tip to vulva anlage 33–53  $\mu\text{m}$ . Gonad primordium with four to eight cells. Anus faint. Tail tip pointed. Adult infective stage enclosed within the fourth stage.

#### Hosts

Diptera: *Lutzomyia* (Psychodidae).

#### Type species

*Anandranema phlebotophagum* Poinar, Ferro, Morales & Tesh, 1993

No other species.

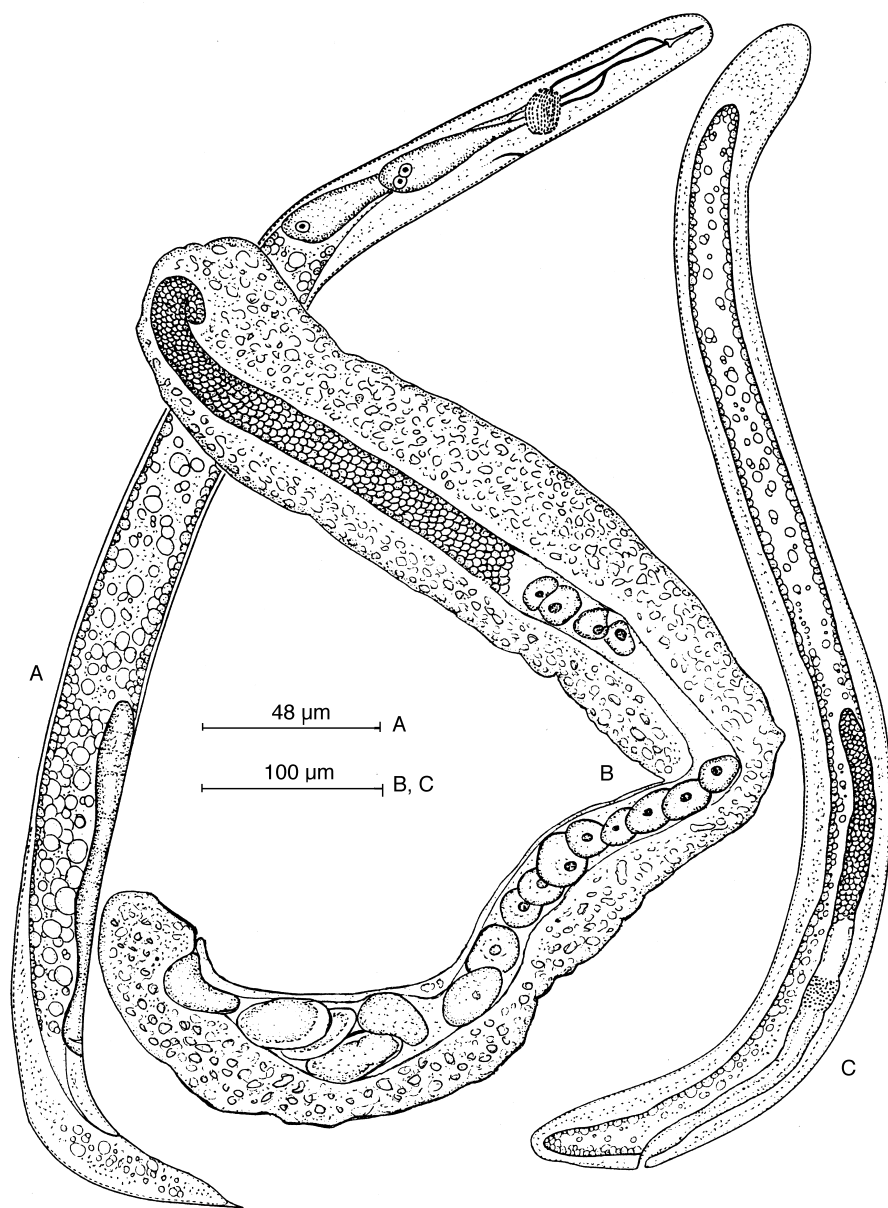
#### Remarks

*Anandranema* is unique among the members of the family in having hermaphrodites in place of females and males. The small body size and inconspicuous vulva in infective hermaphrodites and pleomorphic parasitic hermaphrodites are characteristics of the genus.

ETYMOLOGY. From the Greek noun *anandros* = husbandless, and *nema* = nematode.

The type species was found parasitizing *Lutzomyia longipalpis* (Phlebotominae, Psychodidae) in a laboratory colony originating from Colombia.





**Fig. 150.** *Anandranema phlebotophagum* Poinar *et al.* A. Infective stage hermaphrodite. B. Mature parasitic hermaphrodite. C. Immature parasitic hermaphrodite. (After Poinar *et al.*, 1993.)

## Genus *Bradynema* zur Strassen, 1892

(Fig. 148, G–K)

### Diagnosis

Allantonematinae. **Entomoparasitic forms: Female:** Body elongate-saccate with rounded ends, 5–7 mm long ( $a < 8$ ) in type species, but may be 1–2 mm (*Bradynema trixagi*) to 12–15 mm (*B. strasseni*) long; metabolic by-products white or transparent. Cuticle and hypodermis transversed by fine canals (= food canals). **Stylet absent.** Vulva near anus; lip distinct. Uterus saccate, may occupy up to 85% of body cavity, with eggs and juveniles. Ovary short, outstretched or reflexed. Tail short, bluntly rounded. Ovoviviparous. Juveniles leave the host via the rectum or are deposited with the insect eggs. **Partially free-living forms: Female:** Body slender, 0.4–1 mm long, not dorsally curved. Cuticle smooth. Cephalic region faintly set off. Stoma region slightly cuticularized. **Stylet absent.** Dorsal gland opens near base of stoma region. Oesophagus cylindroid; glands extending near to middle of body. Vulva near anus, lips not raised. Postvulval uterine sac absent. Ovary under-developed. Tail short, conoid-rounded or cylindroid, straight or ventrally arcuate. **Male:** As long as or slightly smaller than female. **Stylet absent.** Oesophagus and its glands degenerate. Testis outstretched; vas deferens packed with hundreds of minute sperm. Spicules small (12–16  $\mu\text{m}$  long), broad, cephalated, distally pointed. Gubernaculum present. Tail conoid. Bursa absent (except in *B. trixagi* which has a bursa enveloping tail).

### Hosts

Coleoptera: *Aphodius*, *Spondylis*, *Throscus*.

Diptera: *Bibio*.

Hemiptera: *Gerris*, *Nepa*, *Velia*.

Siphonaptera: *Ctenophthalmus*.

### Type species

*Bradynema rigidum* (von Siebold, 1836) zur Strassen, 1892

syn. *Filaria rigida* von Siebold, 1836

*Allantonema rigidum* (von Siebold) Moniez, 1891

### Other species

*Bradynema bibionis* Wachek, 1955

*B. gerridis* Poisson, 1933

*B. kurochkini* Rubzov & Tshumakova in Rubzov, 1981

*B. nepae* Poisson, 1933

*B. strasseni* Wülker, 1923

*B. trixagi* Wachek, 1955

*B. veliae* Poisson, 1933

The type species parasitizes the body cavity of *Aphodius fimetarius* L. in Denmark, Germany and Czechoslovakia. The incidence of infection in Denmark was 0–35% and up to 25 gravid females were found in one beetle (Bovien, 1937). The juveniles were also found in the body cavity of hibernating beetles and in the soft tissue of the

elytra. The species was studied in detail by zur Strassen (1892), Wülker (1923) and Wachek (1955). *Bradynema bibionis* in a dipteran, *Bibio* sp., was found in 42% of the population in Erlangen (Germany) in 1951. *Bradynema trixagi* was found in 27% of the population of a coleopteran, *Throscus dermestoides* L., also in Germany; up to 15 parasitic females per host were found (Wachek, 1955). *Bradynema gerridis*, *B. nepae* and *B. veliae* occurred in France.

### Genus *Thripinema* Siddiqi, 1986

(Fig. 151)

#### Diagnosis

Allantonematinae. **Entomoparasitic female:** Body small, oval (0.15–0.23 mm long;  $a = 1.6$ –1.8 in type species), with or without a tail peg, striated. Stylet 10–13  $\mu\text{m}$  long, **lacking basal knobs**. Oesophagus atrophied. Vulva terminal or subterminal. Ovary occupying most of body cavity, with three to four flexures; oogonia arranged about a rachis. Spermatheca with pouch-like structures containing minute sperm. **One or two eggs in uterus at one time. Oviparous.** The juveniles mature in the host and leave via oviduct as fully developed, free-living forms. **Partially free-living forms: Female: In flowers, buds and leaf-galls.** Straight to arcuate upon relaxation, small (0.25–0.29 mm long,  $a = 20$ –27). Cuticle finely striated. **Stylet strong, without basal knobs** (except in *T. khrustalevi*). Orifices of dorsal and subventral oesophageal glands at 2.6–3 and 3–3.6 stylet lengths from anterior end, respectively. Oesophagus fusiform; glands elongated, extending to two-thirds of body length. Vulva inconspicuous. Ovary immature, anteriorly outstretched. Uterus packed with sperm. **Male:** Body straight to arcuate, 0.23–0.33 mm long;  $a = 16$ –20;  $c = 12$ –15. **Stylet absent.** Oesophagus degenerated. Testis extending to oesophageal region. Tail subcylindroid-subclavate, about three anal body widths long. Spicules arcuate, pointed, 14–16  $\mu\text{m}$  long. Gubernaculum 4–5  $\mu\text{m}$  long, weakly developed. **Bursa prominent, adanal or almost terminal.**

#### Hosts

Thysanoptera: *Aptinothrips*, *Frankliniella*, *Megaluriothrips*, *Taeniothrips*.

#### Type species

*Thripinema reniraoi* Siddiqi, 1986

syn. *Howardula aptini* apud Reddy, Nickle & Rao, 1982

*Howardula reniraoi* (Siddiqi, 1986) Ebsary, 1991

#### Other species

*Thripinema aptini* (Sharga, 1932) Siddiqi, 1986

syn. *Tylenchus aptini* Sharga, 1932

*Anguillulina aptini* (Sharga) Lysaght, 1935

*Howardula aptini* (Sharga) Wachek, 1955

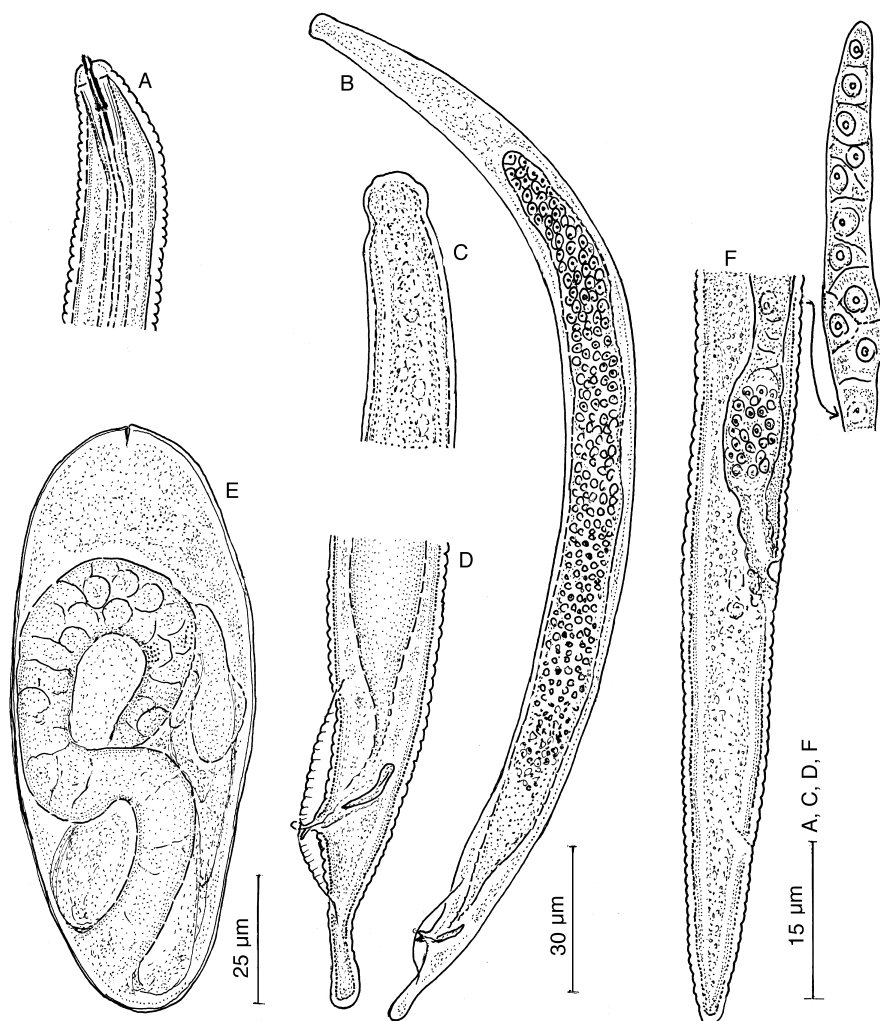
*T. fuscum* Tipping & Nguen in Tipping, Nguen, Funderburk & Smart, 1998

*T. khrustalevi* Chizhov, Subbotin & Zakharenkova, 1995

*T. nicklewoodi* Siddiqi, 1986

syn. *Howardula aptini* apud Nickle & Wood, 1964

*Howardula nicklewoodi* (Siddiqi, 1986) Ebsary, 1991



**Fig. 151.** *Thripinema reniraoi* Siddiqi, 1986. A and F. Anterior and posterior ends of partially free-living, impregnated female. B. Male. C and D. Anterior and posterior ends of male. E. Entomoparasitic female from the haemocoel of *Megalurothrips* sp. in India. (B. Holotype, remainder paratypes.)

## Remarks

*Thripinema* Siddiqi, 1986 differs from *Howardula* Cobb, 1921 in having small oval parasitic females, and the male having an adanal bursa, subclavate tail, and in parasitizing thrips. It differs from *Allantonema* Leuckart, 1884 in having smaller parasitic females having one or two eggs in the uterus at one time, a different host range and the male with adanal bursa and no stylet. *Thripinema* has free-living stages in flowers, buds and leaf galls (cf. *Fergusobia*).

*Thripinema reniraoi* differs from *T. aptini* in having much smaller mature females (0.266–0.316 mm long in *T. aptini*), a shorter bursa not extending to near terminus and spicules being shorter than anal body width. The specific epithet is derived from Reddy, Nickle and Rao, the authority of the type species name. *Thripinema nicklewoodi* is recognized from the other two species of the genus in having mature females with a conical head end and the male with a non-clavate tail, an almost terminal bursa and the proximal end of the gubernaculum appearing in lateral view as a shepherd's crook. This species is named after W.R. Nickle and G.W. Wood, who first described it in 1964 as *Howardula aptini* (Sharga). Reddy *et al.* (1982) foresaw the recognition of the above three species.

ETYMOLOGY. Prefix from host's family name Thripidae, and *nema* = nematode.

The type species was found parasitizing *Megaluriothrips* sp. infesting the flowers of leguminous crops in Andhra Pradesh, India. In adult hosts, one to six adult nematodes, 260–320 juveniles and 280–420 eggs were found. Males and fourth-stage females emerge through the ovipositor of the thrip. Copulation takes place in the flower buds. The parasitized thrips had damaged and reduced ovaries, thus the nematode can be used for biological control of *Megaluriothrips* sp. which damages leguminous crops (Reddy *et al.*, 1982).

*Thripinema aptini* was found by Sharga (1932) in the vicinity of Edinburgh, UK, parasitizing females of *Aptinothrips rufus* Gmelin; the lowest infection (12.3%) was in March and the highest (37.5%) in July. Infested thrips had degenerate ovaries and were incapable of producing eggs. Lysaght (1936) studied the life cycle of this species.

Nickle & Wood (1964) reported that the free-living males and females of *T. nicklewoodi* probably mate in the leaf-galls initiated by the thrips. The fertilized female attacks the thrip larva or pupa. *Thripinema nicklewoodi* represented 88.3% of all natural enemies of *Franklinia occidentalis* on ornamentals within its presumed centre of origin in California, USA (Heinz *et al.*, 1996). *Thripinema fuscum* is a parasite of tobacco thrips, *Frankliniella fuscus*, collected from peanuts in Florida, USA. Chizhov *et al.* (1995) recovered specimens of *T. khrustalevi* from thrips (*Thrips trehernei* and *T. physopus*) associated with the flowers of *Taraxacum officinale* and *Hieracium* spp. (Compositae) in Moscow lawns. They found that the parasitic female of *Thripinema khrustalevi* lacked a cuticle and the integument was provided with microvilli for food absorption. They gave a key to the species of *Thripinema*.

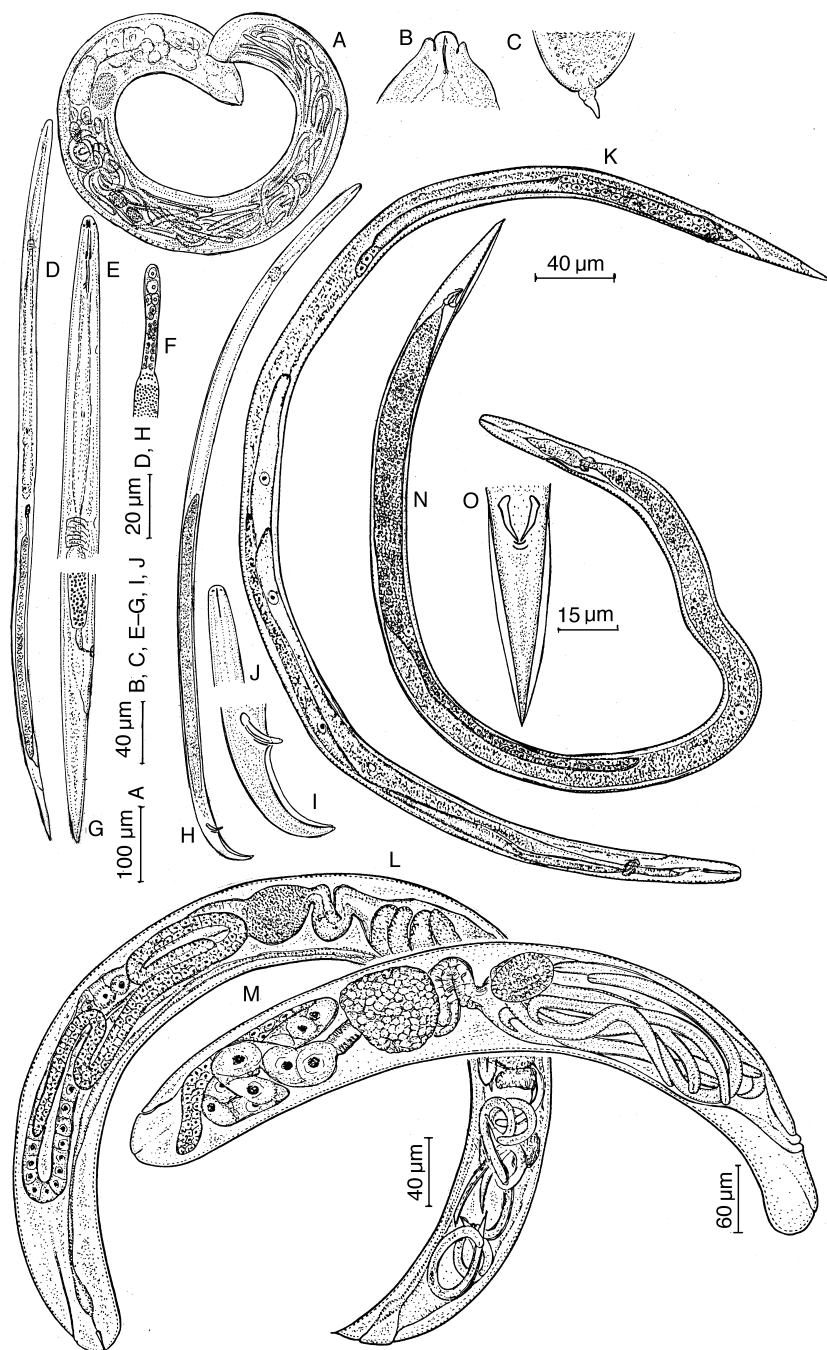
### Genus *Metaparasitylenchus* Wachek, 1955 (Nickle, 1967)

syn. *Parasitylenchus* (*Metaparasitylenchus* Wachek, 1955)

(Fig. 152. A–J)

#### Diagnosis

Allantonematinae. **Entomoparasitic female:** Body obese, cylindroid, straight or slightly arcuate, inert or with slight mobility, white, occasionally with yellow-brown metabolic deposits, 0.8–11 mm long. Cephalic region and tail deformed by body expansion. Cuticle may be coarsely annulated and wrinkled, but body surface not wavy or with swollen areas. **Stylet knobbed, usually sunken in body.** Uterus



**Fig. 152.** A–J. *Metaparasitylenchus guadeloupensis* Laumond & Mauléon. A–C. Parasitic female from host. D–G. Preadult infective female. H–J, N, O. Free-living male. K–O. *Psyllotylenchus viviparus* Poinar & Nelson. K. Preadult infective parasitic female. L. Gamogenetic female from host. M. Parthenogenetic female from host. (A–J. Modified after Laumond & Mauléon (1982). K–O. Modified after Poinar & Nelson (1973).)

enormous, filling most of body cavity. Ovary coiled in anterior region. Tail end conoid-rounded, with or rarely without a peg-like projection. Generally ovoviviparous. No male or complete generative cycle in host. Juveniles leave host after second moult; third moult occurs in free life, but not the fourth moult. **Partially free-living forms: Free life short. Female:** Preadult still within the juvenile cuticle; after fertilization invades host's larva or pupa and moults for the last time. About 0.4–0.8 mm long, with longish conoid-rounded tail, tail end generally straight. **Stylet stout, with well-developed knobs**, 9–17  $\mu\text{m}$  long. **Excretory pore at anterior margin of nerve ring or more anterior**, less than 70  $\mu\text{m}$  from anterior end. Vulva near anus, ovary rudimentary. **No postvulval uterine sac or postrectal intestinal sac. Male:** About as long as or longer than female. Stylet weaker and smaller than that of female, 8–11  $\mu\text{m}$  long. Spicules cephalated, 12–17  $\mu\text{m}$  long. Gubernaculum present. **Tail fairly long, enveloped by a large bursa.**

### Hosts

Coleoptera (mostly other than bark beetles): *Cossonus*, *Cryptophagus*, *Elmis*, *Leperisinus*, *Limnius* (= *Latelmis*), *Mycetophagus*, *Riolus*, *Rhizophagus*, *Scolytodes* (= *Hexacolus*), *Strangalia*, *Telmatophilus*, *Tetropium*.

### Type species

*Metaparasitylenchus telmatophili* (Wachek, 1955) Nickle, 1967  
syn. *Parasitylenchus* (*Metaparasitylenchus*) *telmatophili* Wachek, 1955

### Other species

*Metaparasitylenchus boopini* (Wachek, 1955) Siddiqi, 1986  
syn. *Parasitylenchus* (*Proparasitylenchus*) *boopini* Wachek, 1955  
*Proparasitylenchus boopini* (Wachek) Nickle, 1967  
*M. cossoni* (Wülker, 1929) Nickle, 1967  
syn. *Parasitylenchus cossoni* Wülker, 1929  
*M. cryptophagi* (Wachek, 1955) Nickle, 1967  
syn. *Parasitylenchus* (*Metaparasitylenchus*) *cytrophagi* Wachek, 1955  
*M. guadeloupensis* Laumond & Mauléon, 1982  
*M. helmidis* (Wachek, 1955) Nickle, 1967  
syn. *Parasitylenchus* (*Metaparasitylenchus*) *helmidis* Wachek, 1955; nec *P. helmidis* Stammer, 1934 (= nomen nudum, Wachek, 1955)  
*M. leperisini* (Massey, 1974) Siddiqi, 1986  
syn. *Parasitylenchus leperisini* Massey, 1974  
*M. mycetophagi* (Wachek, 1955) Nickle, 1967  
syn. *Parasitylenchus* (*Metaparasitylenchus*) *mycetophagi* Wachek, 1955  
*M. oschei* (Rühm, 1956) Nickle, 1967  
syn. *Parasitylenchus* (*Metaparasitylenchus*) *oschei* Rühm, 1956  
*M. rhizophagi* (Wachek, 1955) Nickle, 1967  
syn. *Parasitylenchus* (*Metaparasitylenchus*) *rhizophagi* Wachek, 1955  
*M. strangaliae* (Wachek, 1955) Nickle, 1967  
syn. *Parasitylenchus* (*Metaparasitylenchus*) *strangaliae* Wachek, 1955  
*M. tetropii* (Wachek, 1955) Nickle, 1967  
syn. *Parasitylenchus* (*Metaparasitylenchus*) *tetropii* Wachek, 1955

ETYMOLOGY. From the Greek *meta* = after, and *Parasitylenchus*.

The type species parasitized the haemocoel of *Telmatophilus caricis* (Olivier) and *T. typhae*; 27% of the population in Erlangen, Germany, was infected. About 7% of the *Cryptophagus* population was parasitized by *M. cryptophagi* in Germany; 2000–2500 juveniles were recovered from one insect. In Guadeloupe, West Indies, up to 50% of the population of *Scolytodes* (= *Hexacolus*) *guyanensis* (Schedl), a pest of mahogany trees, was parasitized; all larval stages and the pupa could be infected.

**Genus *Sulphuretylenchus* Rühm, 1956 (Nickle, 1967)**

**syn. *Parasitylenchus* (*Sulphuretylenchus* Rühm, 1956)**

(Fig. 153)

**Diagnosis**

Allantonematinae. **Entomoparasitic female:** Body obese, elongate-tuboid, with rounded ends; surface usually **wavy with constrictions and swollen areas** at times due to accumulation of eggs and juveniles; **sulphur yellow-brown to dark brown** (colour bleached by fixatives); 1.1–7.2 mm long. Stylet sunken into body, conus usually asymmetrical and basal knobs flattened laterally; 9–16 µm long. Oesophagus and intestine degenerate; anus obscure, often terminal. Vulva often distinct. Uterus large, with numerous eggs and sometimes early-stage juveniles. Ovary reflexed one to several times, often reaching oesophageal region. Oviparous or ovoviviparous. Male not found in host's body. **Partially free-living forms: Female: Longer (1–1.4 mm) and vulva–anus distance greater than in most allantonematids. Stylet knobbed**, about 10–12 µm long, with distinct lumen. Oesophagus cylindroid. **Excretory pore behind nerve ring, generally 100 µm or more from anterior end.** Vulva–anus distance generally greater than in neoparasitylenchs. Tail cylindroid, tapering to rounded terminus. **Male:** Stylet present. Spicules about 13–14 µm long. Gubernaculum small. Bursa enveloping tail which is elongate-conoid and generally longer than that of neoparasitylenchs.

**Hosts**

Coleoptera (bark beetles): *Dendroctonus*, *Dryocoetes*, *Hylastes*, *Ips*, *Pityogenes*, *Poligraphus*, *Pseudohylesinus*, *Scolytus*.

**Type species**

*Sulphuretylenchus sulphureus* (Fuchs, 1938) Nickle, 1967

syn. *Parasitylenchus sulphureus chalcographi* Fuchs, 1938

**Other species**

*Sulphuretylenchus elongatus* (Massey, 1958) Nickle, 1967

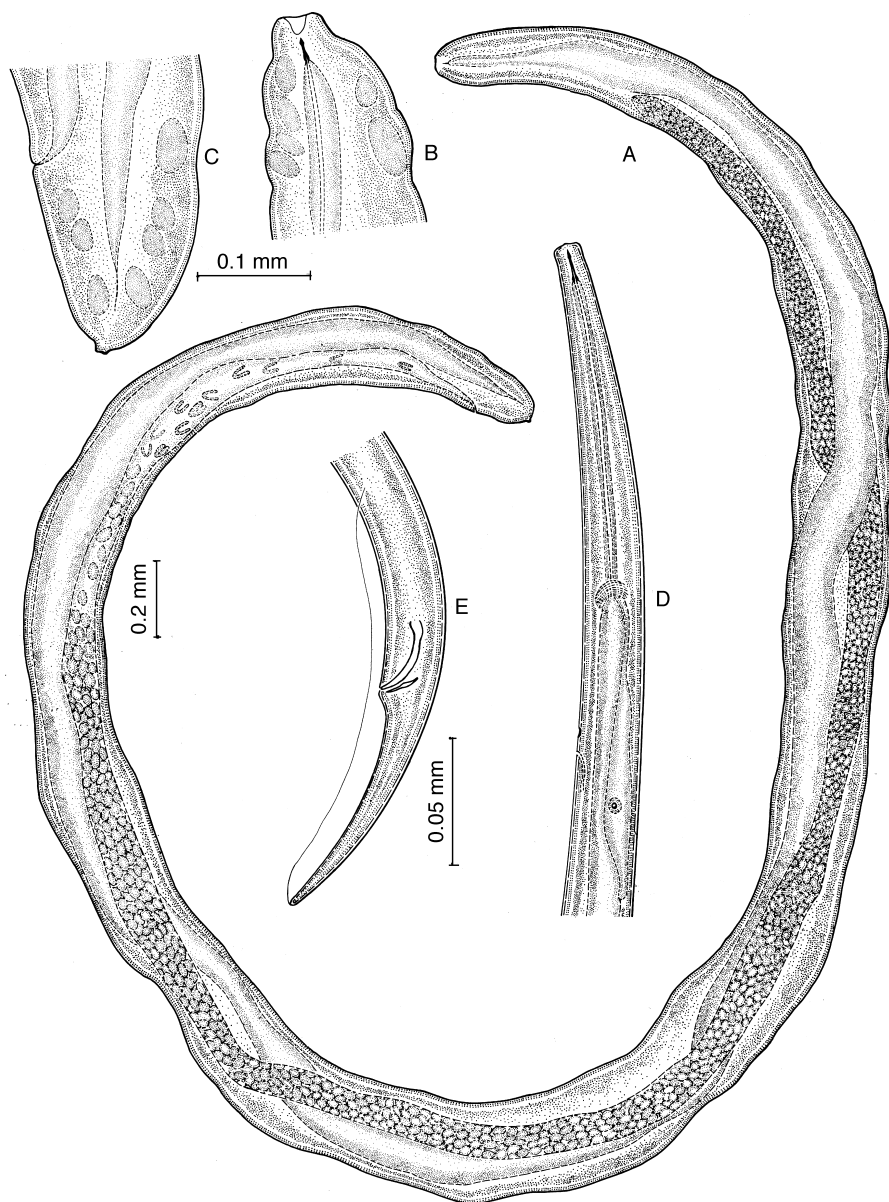
syn. *Parasitylenchus elongatus* Massey, 1958

*S. escherichi* (Rühm, 1956) Nickle, 1967

syn. *Parasitylenchus* (*Sulphuretylenchus*) *escherichi* Rühm, 1956

*S. fuchsi* (Rühm, 1956) Nickle, 1967





**Fig. 153.** *Sulphuretylenchus stipatus* (Massey). A. Mature parasitic female from host. B and C. Head and tail ends of parasitic female, respectively. D and E. Anterior and posterior ends of free-living male, respectively. (After Massey (1974), courtesy US Department of Agriculture, Forest Service.)

- syn. *Parasitylenchus sulphureus poligraphi* Fuchs, 1938 (name a primary junior homonym of *Parasitylenchus dispar poligraphi* Fuchs, 1938 (now *Neoparasitylenchus poligraphi*))  
*Parasitylenchus (Sulphuretylenchus) fuchsi* Rühm, 1956  
*S. grosmanae* (Rühm, 1954) Nickle, 1967  
 syn. *Parasitylenchus grosmanae* Rühm, 1954  
*S. kleinei* (Rühm, 1956) Nickle, 1967  
 syn. *Parasitylenchus (Sulphuretylenchus) kleinei* Rühm, 1956  
*S. nopimigi* Tomalak, Welch & Galloway, 1989  
*S. pilifrons* (Massey, 1958) Nickle, 1967  
 syn. *Parasitylenchus pilifrons* Massey, 1958  
*S. posteruteri* Tomalak, Welch & Galloway, 1989  
*S. pseudoundulatus* Tomalak, Welch & Galloway, 1989  
*S. pugionifer* Slankis, 1969  
*S. stipatus* (Massey, 1966) Siddiqi, 1986  
 syn. *Parasitylenchus stipatus* Massey, 1966  
*S. undulatus* (Massey, 1974) Siddiqi, 1986  
 syn. *Parasitylenchus undulatus* Massey, 1974

## Remarks

*Sulphuretylenchus elongatus*, a parasite of the fir engraver (*Scolytus ventralis* Le Conte) in the USA, emerges as juveniles from the host through anal, genital and oral openings and through intersegmental membranes. Mating occurs in beetle larval galleries. The fertilized female penetrates the cuticle of the host's larva in about 2 h, apparently by the use of the stylet and oesophageal gland enzyme activity. Development of this female is generally synchronized with that of the host. The nematode has a single annual generation. Nematode reproduction occasionally occurred in the host's larva. Parasitism by *S. elongatus* resulted in the host's delayed emergence, limited flight, and aberrant attack behaviour. Female hosts were found to be sterilized by heavy infections (four to five adult nematodes or 1500–3000 juveniles in the haemocoel) and partly sclerotized by light infections (one adult or up to 500 juveniles); parasitism of the male was less severe; some egg and larval mortality occurred due to parasitism (Ashraf & Berryman, 1970).

ETYMOLOGY. From species-group name '*sulphureus*' (for sulphur-coloured parasitic female), and *Tylenchus*.

The type species is parasitic in *Pityogenes chalcographus* (L.), and causes partial sterility, thus reducing the beetle population; 2–4% of beetles were found to be parasitized in Germany.

**Genus *Proparasitylenchus* Wachek, 1955 (Nickle, 1967)****syn. *Parasitylenchus* (*Proparasitylenchus* Wachek, 1955)**

(Fig. 148, L–Q)

**Diagnosis**

Allantonematinae. **Entomoparasitic female:** Body obese, cylindroid, inert or slightly mobile, generally straight to arcuate, 1.2–5.7 mm long; **white or yellow, never brown. Cephalic end projecting** in type species, rarely overgrown by body enlargement, stylet in its normal place. **Tail end conoid, not overgrown** by body enlargement, straight or dorsally turned; anus present. Vulva subterminal or about one vulval body width from tip, lips slightly protuberant. Ovoviviparous. After second moult juveniles reach rectum and escape. **Partially free-living forms:** Two moults in free life; females and males develop in several (14–20) days. **Free life long**, individuals in their habitat resemble free-living neotylenchs. **Female:** About 0.4–0.7 mm long; **tail end generally curved dorsally**. Cephalic region continuous or slightly offset. Stylet 11–15  $\mu\text{m}$  long, **with distinct knobs**, never cleft or bare at base. Orifice of dorsal gland at some distance behind stylet base. Excretory pore behind nerve ring, less than 75  $\mu\text{m}$  from anterior end. A short **rudimentary post-vulval uterine sac generally present**. Intestine generally with a postrectal blind sac. Tail longish, conoid-rounded. Fertilized female invades **host's pupa**. **Male: Generally smaller than female**. Stylet 10–15  $\mu\text{m}$  long, knobbed. Spicules 12–16  $\mu\text{m}$  long. Gubernaculum present. Bursa subterminal in type species, terminal in others.

**Hosts**

Coleoptera (staphylinids): *Anotylus*, *Atheta*, *Carpelimus*, *Medon*, *Oxytelus*, *Platystethus*, *Zyras*.

**Type species**

*Proparasitylenchus platystethi* (Wachek, 1955) Nickle, 1967

syn. *Parasitylenchus* (*Proparasitylenchus*) *platystethi* Wachek, 1955

**Other species**

*Proparasitylenchus athetae* (Wachek, 1955) Nickle, 1967

syn. *Parasitylenchus* (*Proparasitylenchus*) *athetae* Wachek, 1955

*P. medonis* (Wachek, 1955) Nickle, 1967

syn. *Parasitylenchus* (*Proparasitylenchus*) *medonis* Wachek, 1955

*P. myrmedoniae* (Wachek, 1955) Nickle, 1967

syn. *Parasitylenchus* (*Proparasitylenchus*) *myrmedoniae* Wachek, 1955

*P. oxyteli* (Wachek, 1955) Nickle, 1967

syn. *Parasitylenchus* (*Proparasitylenchus*) *oxyteli* Wachek, 1955

*P. trogophloeae* (Wachek, 1955) Nickle, 1967

syn. *Parasitylenchus* (*Proparasitylenchus*) *trogophloeae* Wachek, 1955

**Note**

At present, the following genera – *Proparasitylenchus* Wachek, 1955, *Parasitylenchoides* Wachek, 1955, *Neoparasitylenchus* Nickle, 1967 and *Protylechus* Wachek, 1955 – are poorly demonstrated and can well be considered as subgenera of

*Proparasitylenchus* (see Massey, 1974). This is avoided here as it would entail a large number of new combinations.

ETYMOLOGY. From the Greek *pro* = before, forward, and *Parasitylenchus*.

The type species was found parasitic in the haemocoel of *Platystethus comatus* Grav. with 4.7% of the population infected near Erlangen, Germany.

### Genus *Parasitylenchoides* Wachek, 1955

(Fig. 154, A–I)

#### Diagnosis

Allantonematinae. **Entomoparasitic female:** Obese, cylindroid, arcuate, worm-like, inert or with slight mobility. White, or with yellowish-brown metabolic products, 0.9–6.2 mm long. Cephalic region normal, or overgrown by body enlargement, tail end conoid, with or without a peg-like process; anus visible. Stylet knobbed, 12–16  $\mu\text{m}$  long, usually in normal position. Vulva near anus, lips protuberant. Uterus enormous, sac-like and occupying most of body cavity, with eggs and juveniles, rarely small and tubular in oviparous *P. koeneri*. Ovary coiled. Ovoviviparous, rarely oviparous. Juveniles leave host after two moults via rectum; females of some species (*P. wichmanni*, *P. paromali*, *P. ditomae*) have one moult in free life and the last in the host, but more usually have both moults in free life. **Partially free-living forms:** Free life short or long, juveniles develop to adults in 4–20 days. **Female:** Slender, 0.5–1 mm long, cephalic region slightly offset. **Stylet with distinct knobs**, 9–15  $\mu\text{m}$  long. Orifice of dorsal oesophageal gland 6–8  $\mu\text{m}$  behind stylet base in the type species, but may be closer. **Excretory pore behind nerve ring, 105–125  $\mu\text{m}$  from anterior end.** Vulva near anus. Uterus elongate, acts as receptaculum seminis. Ovary immature, rudimentary postvulval uterine sac absent in type species, but may be present. Tail conoid-rounded or pointed, three body widths or less long; tail end straight, rarely bent dorsally. **Male:** Generally smaller than female. Stylet weaker and smaller than that of female. Oesophagus degenerate. Testis outstretched or reflexed. Gubernaculum small. Bursa well developed, enveloping entire tail.

#### Hosts

Coleoptera: *Aleochara*, *Anotylus*, *Ditoma*, *Micromaethus*, *Oxytelus*, *Paederus*, *Paramalus*, *Plegaderus*, *Sciodrepa*, *Stenus*.

#### Type species

*Parasitylenchoides steni* Wachek, 1955

#### Other species

*Parasitylenchoides ditomae* Wachek, 1955

*P. koeneri* Wachek, 1955

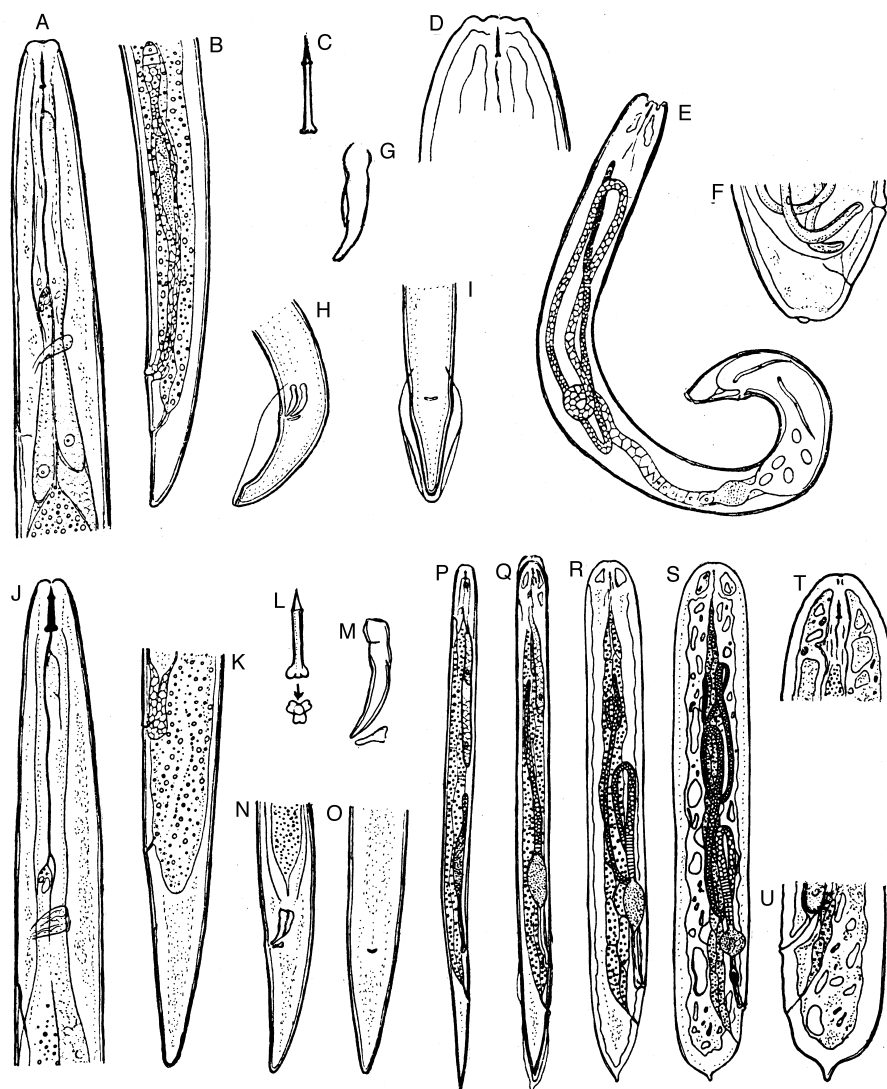
*P. paederi* Wachek, 1955

*P. paromali* Wachek, 1955

*P. rheocharae* Wachek, 1955

*P. sciodrepae* Wachek, 1955

*P. wichmanni* Wachek, 1955



**Fig. 154.** A–I. *Parasytylenchoides steni* Wacheck. J–U. *Protylechus heteroceri* Wacheck. A–C, J and K. Preadult infective females. D–F and P–U. Gametogenetic females from host. G–I and M–O. Free-living males. A and J. Oesophageal regions. B and K. Posterior regions of infective female. C and L. Stylet. D and T. Head ends of female. E and P–S. Entire worms. F and U. Posterior regions of female. G and M. Spicule. H, I, N and O. Tail ends of male. (A–U. Redrawn after Wacheck, 1955.)

**ETYMOLOGY.** From *Parasytylenchus*, and the Greek *oides* = shape, similar.

The type species parasitizes the haemocoel of *Stenus biguttatus* (L.) and other *Stenus* spp. in Germany; about 6% of the insect population was infected near Erlangen.

**Genus *Protylenchus* Wachek, 1955**

(Fig. 154, J–U)

**Diagnosis**

Allantonematinae. **Entomoparasitic female:** Obese, cylindrical, **straight**, 1.4–2.8 mm long, **less than eight times as long as wide**, extremities not overgrown by expansion; **stylet sunken into body**, knobbed. Ovary long, coiled, pushed by uterus into anterior region in viviparous species (*P. anobii*); uterus narrow, tubular in oviparous type species. Juveniles have three moults in host, exit through rectum. **Partially free-living forms:** Juveniles moult a third time to develop into males and females, which mate, in free life. The fertilized female then penetrates the pupa or larva and moults once more. **Female:** 0.54–0.76 mm long. Cephalic region continuous or slightly offset. Stylet well developed, 10–12  $\mu\text{m}$  long, **with prominent knobs** which may be cleft. Orifice of dorsal gland at over half stylet length behind stylet knobs. **Excretory pore over 100  $\mu\text{m}$  from anterior end, behind nerve ring.** Postvulval uterine sac absent. Postrectal intestinal sac present. Tail conoid-rounded, two to three times anal body width long; tail end straight to ventrally arcuate. **Male:** Slightly smaller than female. Cephalic region, stylet and tail as in female. Spicules 13–15  $\mu\text{m}$  long. Gubernaculum present, proximally thickened in type species. **Bursa absent.**

**Hosts**Coleoptera: *Heterocerus*, *Anobium*.**Type species***Protylenchus heteroceri* Wachek, 1955**Other species***Protylenchus anobii* (Wachek, 1955) Siddiqi, 1986syn. *Parasitylenchoides anobii* Wachek, 1955ETYMOLOGY. From the Greek *pro* = before, forward, and *Tylenchus*.

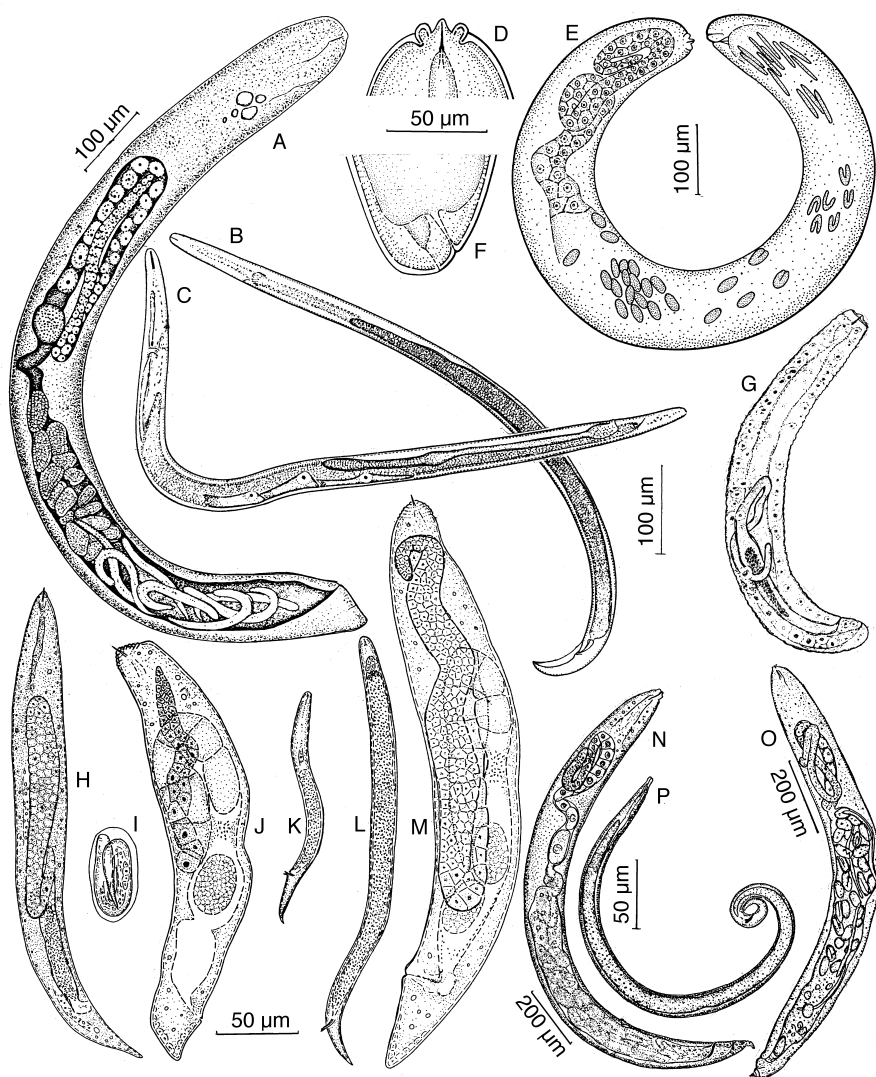
The type species was found near Erlangen, Germany, parasitizing *Heterocerus marginatus* (Fabricius) and *H. fenestratus* (Thunberg). About 17–23% of the population was infected, and up to 4500 juveniles could occur at one time in the haemocoel.

**Genus *Neoparasitylenchus* Nickle, 1967**syn. subgen. *Neoparasitylenchus* Nickle, 1963 (nom. nud.)

(Fig. 155, A–G)

**Diagnosis**

**Entomoparasitic forms:** No generative cycle in host (cf. *Parasitylenchus*). **Female:** Body obese, sausage- or worm-shaped, usually curved, inert or slightly mobile, usually 0.5–2.5 mm long. Cephalic region overgrown by body enlargement. Body white, turning yellowish brown to light brown due to metabolic products. Stylet generally



**Fig. 155.** A–C. *Neoparasitylenchus amylocercus* Poinar & Caylor. D–F. *Neoparasitylenchus avulsi* (Massey). G. *Neoparasitylenchus cryphali* (Fuchs). H–M. *Parasitylenchus diplogenus* Welch. N–P. *Parasitylenchus coccinellinae* Iperti & Waerebeke. A, E, G, M and N. Adult gamogenetic females from host's haemocoel. B and K. Free-living males. C. Partially free-living infective female. D. Head cone of adult gamogenetic female. F. Tail end of adult gamogenetic female. H. Preadult gamogenetic female from haemocoel of *Drosophila subobscura* Col. I. Embryonated egg. J and O. Secondary parasitic females from host's haemocoel. L and P. Males of parasitic generation from host's haemocoel. (Modified: A–C. After Poinar & Caylor (1974). D–F. After Massey (1974). G. After Fuchs (1914). H–M. After Welch (1959). N–P. After Iperti & van Waerebeke (1968).)

13–16  $\mu\text{m}$  long, **not sunken into body**. Vulva subterminal. Uterus enormous, with numerous eggs and juveniles; ovary coiled, pushed into anterior region. Anus terminal or subterminal, tail end usually obtusely rounded, with or without a peg-like projection. Oviparous or ovoviviparous. Juveniles with weakly developed gonad leave host shortly before third and last moult, and develop to adult in a few days. **Partially free-living forms:** Free life short. Body vermiform, about 0.4–0.7 mm long. Cephalic region continuous or slightly offset. Stylet generally 14–15  $\mu\text{m}$  long, with **slight basal thickenings**. Orifice of dorsal gland usually at a distance from stylet base. **Excretory pore behind nerve ring**. Vulva at about 90–95% of body length. Ovary immature but with more cells than in *Allantonema* and *Contortylenchus*. Postvulval uterine sac rudimentary or absent. Tail conoid, pointed or minutely rounded. Fertilized female invades **host's larva**. Male about the size of the female. Spicules small, cephalated. Gubernaculum present. Bursa distinct, enveloping entire tail.

### Hosts

Coleoptera (bark beetles): *Blastophagus*, *Conophthorus*, *Cryphalus*, *Crypturgus*, *Dendroctonus*, *Dryocoetes*, *Hylesinus*, *Hylurgops*, *Hylurgus*, *Hylastes*, *Ips*, *Pissodes*, *Pityogenes*, *Pityophthorus*, *Polygraphus*, *Scolytus*, *Xyleborus*.

### Type species

*Neoparasitylenchus cryphali* (Fuchs, 1914) Nickle, 1967  
 syn. *Tylenchus dispar cryphali* Fuchs, 1914  
*Parasitylenchus dispar* var. *cryphali* (Fuchs) Micoletzky, 1922  
*Aphelenchulus cryphali* (Fuchs) Filipjev, 1934  
*Parasitylenchus* (*Parasitylenchus*) *cryphali* (Fuchs) Rühm, 1956

### Other species

*Neoparasitylenchus amvolocercus* Poinar & Caylor, 1974 (original spelling *amvolocercus*)  
*N. avulsi* (Massey, 1958) Nickle, 1967  
 syn. *Parasitylenchus avulsi* Massey, 1958  
*N. betulae* (Rühm, 1956) Nickle, 1967  
 syn. *Parasitylenchus* (*Parasitylenchus*) *betulae* Rühm, 1956  
*N. brachydorus* Slankis, 1974  
*N. caveocaudatus* Slankis, 1974  
*N. chalcographi* (Fuchs, 1938) Nickle, 1967  
 syn. *Parasitylenchus dispar chalcographi* Fuchs, 1938  
*N. cinerei* (Fuchs, 1929) Nickle, 1967  
 syn. *Tylenchus dispar cinerei* Fuchs, 1929  
*Aphelenchulus cinerei* (Fuchs) Filipjev, 1934  
*Parasitylenchus* (*Parasitylenchus*) *cinerei* (Fuchs) Rühm, 1956  
*Parasitylenchus dispar pusilli* Fuchs, 1938  
*N. coronatus* (Massey, 1974) Siddiqi, 1986  
 syn. *Parasitylenchus coronatus* Massey, 1974  
*N. hylastis* (Wülker, 1923) Nickle, 1967  
 syn. *Tylenchus hylastis* Wülker, 1923  
*Parasitylenchus hylastis* (Wülker) Filipjev, 1934



- Tylenchus dispar ater* Fuchs, 1929  
*Tylenchus dispar cunicularii* Fuchs, 1929  
*Parasitylenchus hylurgi* Filipjev, 1934  
*N. ipinus* (Massey, 1974) Siddiqi, 1986  
     syn. *Parasitylenchus ipinus* Massey, 1974  
*N. ligniperdae* (Fuchs, 1929) Nickle, 1967  
     syn. *Tylenchus ligniperdae* Fuchs, 1929  
     *Parasitylenchus ligniperdae* (Fuchs) Filipjev, 1934  
*N. notati* (Fuchs, 1929) Siddiqi, 1986  
     syn. *Tylenchus sulphureus notati* Fuchs, 1929  
*N. oriundus* (Massey, 1974) Siddiqi, 1986  
     syn. *Parasitylenchus oriundus* Massey, 1974  
*N. orthotomici* (Rühm, 1960) Nickle, 1967  
     syn. *Parasitylenchus* (*Parasitylenchus*) *orthotomici* Rühm, 1960  
*N. ovarius* (Massey, 1958) Nickle, 1967  
     syn. *Parasitylenchus ovarius* Massey, 1958  
*N. parasitus* (Massey, 1974) Siddiqi, 1986  
     syn. *Parasitylenchus parasitus* Massey, 1974  
*N. pessonii* (Rühm in Rühm & Chararas, 1957) Nickle, 1967  
     syn. *Parasitylenchus* (*Parasitylenchus*) *peysonii* Rühm in Rühm & Chararas, 1957  
*N. pityophthori* (Rühm, 1956) Nickle, 1967  
     syn. *Parasitylenchus* (*Parasitylenchus*) *pityophthori* Rühm, 1956  
*N. poligraphi* (Fuchs, 1938) Nickle, 1967  
     syn. *Parasitylenchus dispar poligraphi* Fuchs, 1938  
*N. raphidophorus* Slankis, 1974  
*N. rugulosi* (Schvester, 1957) Nickle, 1967  
     syn. *Parasitylenchus dispar rugulosi* Schvester, 1957  
     *Parasitylenchus* (*Parasitylenchus*) *rugulosi* Schvester (Rühm, 1960)  
*N. scolyti* (Oldham, 1930) Nickle, 1967  
     syn. *Parasitylenchus scolyti* Oldham, 1930  
     *Parasitylenchus secundus* Fuchs, 1933  
*N. scrutillus* (Massey, 1974) Siddiqi, 1986  
     syn. *Parasitylenchus scrutillus* Massey, 1974  
*N. senicus* (Massey, 1974) Siddiqi, 1986  
     syn. *Parasitylenchus senicus* Massey, 1974  
*N. wuelkeri* (Rühm, 1956) Nickle, 1967  
     syn. *Parasitylenchus* (*Parasitylenchus*) *wuelkeri* Rühm, 1956  
*N. xylebori* (Schvester, 1950) Nickle, 1967  
     syn. *Parasitylenchus dispar xylebori* Schvester, 1950

## Notes

In the USA, *Neoparasitylenchus avulsi* and *N. ovarius* parasitize *Ips* spp. in Alabama and Colorado, respectively. *Neoparasitylenchus scolyti* was found to parasitize 60% of the populations of *Scolytus scolytus* (Fabricius) (= *S. destructor*) in Britain, 40% of which were sterile.

The fertilized female of *Neoparasitylenchus rugulosi*, a parasite of shothole borer, *Scolytus rugulosus* (Müller), enters the host's larva and grows in the body cavity,

nourished by the haemolymph. As the host becomes adult, the female nematode matures and deposits hundreds of eggs or juveniles in the haemocoel. The juveniles escape from the head end (as opposed to the tail end in several other species) of the host as fourth-stage males and females. They moult in the beetle galleries and mate within 2–3 days. The male dies and the fertilized preadult female seeks out a beetle larva to complete its life cycle. The parasitized beetle makes short galleries, horizontal to the stem, does not lay eggs, and soon dies (Nickle, 1971).

Massey (1974) regarded *Neoparasitylenchus* as a junior synonym of *Parasitylenchus*, but Poinar & Caylor (1974), Slankis (1974) and Poinar (1975) recognized it as valid. Siddiqi (1986) recognized *Parasitylenchus* under a different family, Parasitylenchidae.

ETYMOLOGY. From the Greek *neos* = young, new, and *Parasitylenchus*.

### Genus *Pratinema* Chizhov & Sturhan, 1998

(Fig. 156)

#### Diagnosis

Allantonematinae. **Entomoparasitic female:** Obese, cylindrical, **ventrally curved in a tight spiral**, 1.7–2.9 mm long ( $a = 12$ –26), stylet thin-walled, with distinct lumen, lacking knobs. Ovary long, outstretched, rarely with short loop near middle, extending to near stylet base, with numerous oocytes; uterus narrow, tubular, with several synchronous eggs in a single file. **Vulva slit-like, about one half body-width long.** Vaginal wall thickened. Young females oviparous, old ones viviparous. One parasitic female with numerous eggs and juveniles per host fly. Last-stage juveniles exit through gonad opening to the environment (cow-dung), where they moult to become free-living males and females in about 10–14 days. After being impregnated, infective females attack fly larvae. **Partially free-living forms: Female:** 0.45–0.65 mm long ( $a = 24$ –42). Cephalic region continuous. Stylet well developed with basal thickenings, 9–15 (12)  $\mu\text{m}$  long; conus about one-fourth of stylet length in type species. Orifice of dorsal gland 6–8  $\mu\text{m}$  behind stylet knobs. **Excretory pore wide, duct sclerotized, renette large, opposite oesophageal base.** Hemizonid 8–11  $\mu\text{m}$  anterior to excretory pore. Vulva close to anus, lips not raised. Postvulval uterine sac absent but short sac sometimes seen. Tail elongate, tapering to a slender pointed terminus, 6–13 times anal body width long. **Male:** 0.37–0.47 mm long. Cephalic region continuous, rounded to anteriorly flattened. Stylet 4–5  $\mu\text{m}$  long, with minute basal thickenings. Tail as in female. **Bursa and gubernaculum absent.** Spicules slightly arcuate, cephalated, 11–15 (13)  $\mu\text{m}$  long in type species.

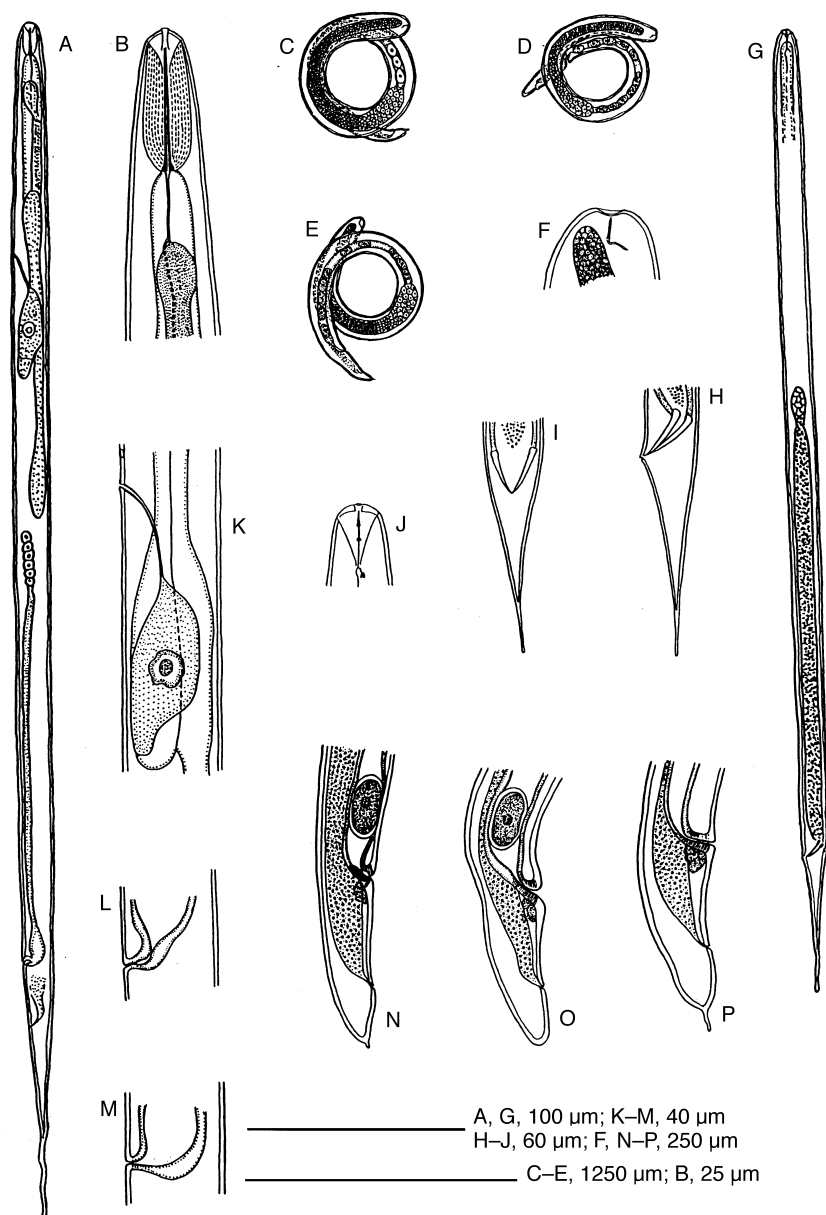
#### Hosts

Diptera: *Sepsis*.

#### Type species

*Pratinema sepsis* Chizhov & Sturhan, 1998.

No other species.



**Fig. 156.** *Pratinema sepsis* Chizhov & Sturhan. A. Infective female. B. Anterior region of infective female. C-E. Body habitus of parasitic females. F. Anterior end of parasitic female. G. Free-living male. H and I. Tail ends of male, lateral and ventral view, respectively. J. Head end of male. K. Excretory system. L and M. Vulval regions of infective females. N-P. Posterior ends of parasitic females. (After Chizhov & Sturhan (1998), courtesy *Russian Journal of Nematology*.)

## Note

*Pratinema* is characterized by having a single bisexual generation, in which copulation takes place in the environment. It shows several characters of Allantonematinae but the parasitic female has a prominent, cleft-like vulva as in members of Contortylenchinae. The body is curved ventrally and spirally, unlike Contortylenchinae with a dorsally curved body. The elongate filiform tails in free-living forms, the sclerotized excretory duct and the male having a stylet and lacking a bursa and gubernaculum further characterize this genus.

ETYMOLOGY. From the Latin *pratium* = lawn, meadow, and *nema* for nematode.

The type species was found in coprophilous flies, *Sepsis punctum* F. (type host) and *Sepsis* sp. (Diptera: Sepsidae), near Borok at the campus of the Institute of Inner Waters Biology, Nekouz district, in Jaroslavl and in Khimki district in the Moscow region.

## Genus *Scatonema* Bovien, 1932

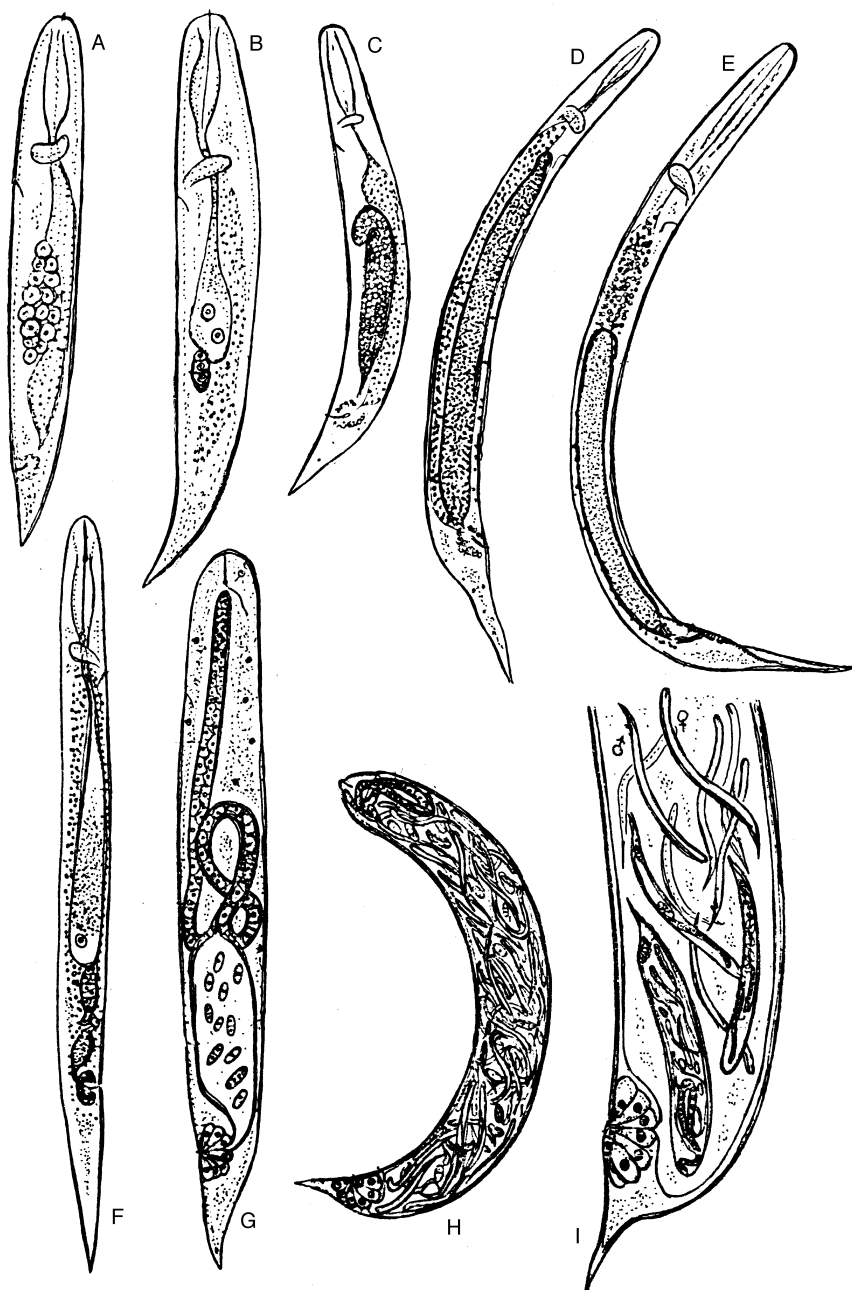
(Fig. 157)

## Diagnosis

Allantonematinae. **Entomoparasitic female: Found in larvae, pupae and imagines of *Scatopse*** and also in maternal body. Torpedo- or sausage-shaped, with conoid-pointed posterior end, varying from 0.4 mm long by 45  $\mu$ m to about 2 mm long by about 85  $\mu$ m wide, obese, with partial mobility; may be strongly arcuate ventrally. Cephalic region short, stump-like. Stylet with basal knobs. Most of the body occupied by uterus packed with eggs and **later with various stages of juveniles and adults; spermatized and gravid females found in maternal body, where they produce a second generation; males occur and copulation takes place in maternal body.** Ovary coiled in anterior region. Sperm aggregate in spermatheca, close to oviduct. Vagina and terminal part of uterus surrounded by large (50–74  $\mu$ m) **perivaginal cells.** Ovoviviparous. Youngest juveniles about 0.127 mm long, a < 8, body torpedo-shaped. Preadult juveniles reach ovary and are deposited with insect's egg clusters of *Scatopse* on manure. About 0.33 mm long, 17  $\mu$ m wide. Cephalic region hexaradiate, continuous, rounded. Stylet 12–16  $\mu$ m long, **with distinct basal knobs.** Oesophagus cylindrical, non-muscular; subventral glands large, extending to midbody region and opening just in front of nerve ring. Excretory pore behind nerve ring. Vulva small, not prominent, at about 75% of body length. Uterus packed with minute sperm, extending for less than two body widths from vagina. Ovary immature, hardly one body width long, reaching near to base of subventral glands. Anus obscure. Tail end conically pointed. Penetrates a larva, pupa or imago of *Scatopse*. **Male:** About 0.35 mm long, 18  $\mu$ m wide. **Stylet absent.** Oesophagus completely degenerate. Testis single, filled with minute sperm. Tail conically pointed, similar to that of the female. Spicules tylenchoid, 11–12  $\mu$ m long. Gubernaculum linear. Bursa distinct, **extending to about middle of tail.**

## Host

Diptera: *Scatopse*.



**Fig. 157.** *Scatonema wuelkeri* Bovien. A and B. Newly hatched male and female juveniles, respectively. C and D. Male juveniles, later stages. E. Male. F. Preadult infective female. G. Female from haemocoel of *Scatopse* sp. larva. H and I. Mature female from host (note juveniles and adults in maternal body cavity). (A–I. Redrawn after Bovien, 1932.)

### Type species

*Scatonema wuelkeri* Bovien, 1932

No other species.

ETYMOLOGY. From prefix of host's name *Scatopse*, and *nema* = nematode.

According to Bovien (1932), *Scatonema wuelkeri* parasitizes larvae, pupae, and imagines of *Scatopse fuscipes* Meigen in Denmark. The nematode is able to reproduce in the host's larvae and is unique in having a second generation produced within the body of its mother. The parasitized *Scatopse* larvae lose their fat body and succumb, the first and second stage being the most severely affected. About 25% of the population of young *Scatopse* larvae was found to harbour female *Scatonema*; in imagines, the incidence of infection was 5–10%; one to four adults were found in individual insects, occasionally as many as 20 adult parasites were found in one host. Rapid development results in the production of the second generation before the *Scatopse* larva is half grown. The preadult juveniles reach the host's ovarioles and are deposited with egg clusters in manure or putrefying organic material, where they grow and mate. Apparently the nematodes remain in the clusters so that the spermated females can penetrate a larva as soon as it hatches.

## Subfamily Contortylenchinae Rühm, 1956

### Diagnosis

Allantonematidae. No complete generation cycle in host or environment. Entomoparasitic female elongate-obese or short obese, crescent-shaped, **dorsally curved and contorted**, rarely straight then with tail end dorsally directed. **Cephalic cone in parasitic female present**. Stylet generally under 10  $\mu\text{m}$  long, knobbed. **Vulva prominent, deeply cleft, in a depression**. Tail end conoid, generally directed dorsally; tail short, may be absent. Oviparous. **Parasites of haemocoel of Coleoptera**. Partially free-living forms with stylet 15  $\mu\text{m}$  or less long, with or without basal knobs. Vulva not prominent; ovary immature. Spicules cephalated, arcuate, under 25  $\mu\text{m}$  long.

### Type genus

*Contortylenchus* Rühm, 1956

### Other genera

*Aphelenchulus* Cobb, 1920

*Bovienema* Nickle, 1963

### Remarks

Rühm (1956) proposed the family Contortylenchidae for his new genus *Contortylenchus*. This family was not recognized by Nickle (1967), Poinar (1975) and Kaya (1984), who placed *Contortylenchus* under the subfamily Allantonematinae. Massey (1974) recognized Contortylenchidae on such characters as the contorted form and homomorphic shape of the body, deeply cleft vulva and the structure of the stylet and other internal organs of the parasitic female. *Aphelenchulus* is doubt-

fully placed in this subfamily. Siddiqi (1986) placed *Spilotylenchus* under this subfamily, but Slobodyanyuk (1999) proposed a family for it and its related genera. Here *Spilotylenchus* is assigned to Spilotylenchinae of the family Parasytlenchidae.

### Key to genera of Contortylenchinae

1. Parasitic female under 0.8 mm long;  $a < 8$  ..... *Bovienema*  
     Parasitic female over 0.8 mm long;  $a > 10$  ..... *Contortylenchus*  
     ..... *Aphelenchulus*

### Genus *Contortylenchus* Rühm, 1956

(Fig. 158, A–G)

#### Diagnosis

Contortylenchinae. **Entomoparasitic female:** Body about 1–6 mm long, elongate-cylindroid, partially obese, **homomorphic, dorsally arcuate or spiral with ventral side always turned out** when relaxed, usually yellow-brown;  $a > 10$ . Cuticle smooth or finely striated, thick and firm, maintaining cylindroid shape of body. Cephalic region conoid-rounded, not deformed or overgrown by body expansion. Stylet moderately strong, 10–15  $\mu\text{m}$  long, with basal knobs or thickenings. Vulva strongly cleft, at about 94–98%. Vagina short, thick-walled. Uterus long, often with several synchronous eggs. Ovary usually reflexed one or more times; oocytes in two or more rows. Intestine well defined. Rectum often obscure. Anus also obscure, ventrally subterminal, terminal or dorsally subterminal, sometimes absent. Tail end dorsally arcuate, with conoid, obtuse or mamillate tip. No males in host. Newly hatched juveniles under 0.4 mm, with small slender stylet with or without basal knobs. **Partially free-living forms:** Found in galleries of host beetles. **Female:** Under 1 mm, slender. Cephalic region usually continuous. Stylet well developed and knobbed. Excretory pore behind nerve ring. Vulva small, lips not distinct. Postvulval uterine sac may be present. Ovary rarely reflexed. Rectum and anus often obscure. **Male:** Generally under 1 mm long. Stylet present, more slender than that of female. Excretory pore behind nerve ring. Testis with or without a flexure. Spicules small, arcuate. Gubernaculum present. Bursa prominent, enveloping entire tail.

#### Hosts

Coleoptera: *Ips*, *Dendroctonus*, *Cryphalus*, *Hylastes*, *Hylurgops*, *Orthotomicus*.

#### Type species

*Contortylenchus diplogaster* (von Linstow, 1890) Rühm, 1956

syn. *Allantonema diplogaster* von Linstow, 1890

*Tylenchus diplogaster* (von Linstow) Fuchs, 1915

*Tylenchus contortus typographi* Fuchs, 1915 (= *Tylenchus contortus contortus* Fuchs, 1915) (nomen nudum in Fuchs, 1914)

*Parasitylenchus contortus typographi* (Fuchs) Micoletzky, 1922

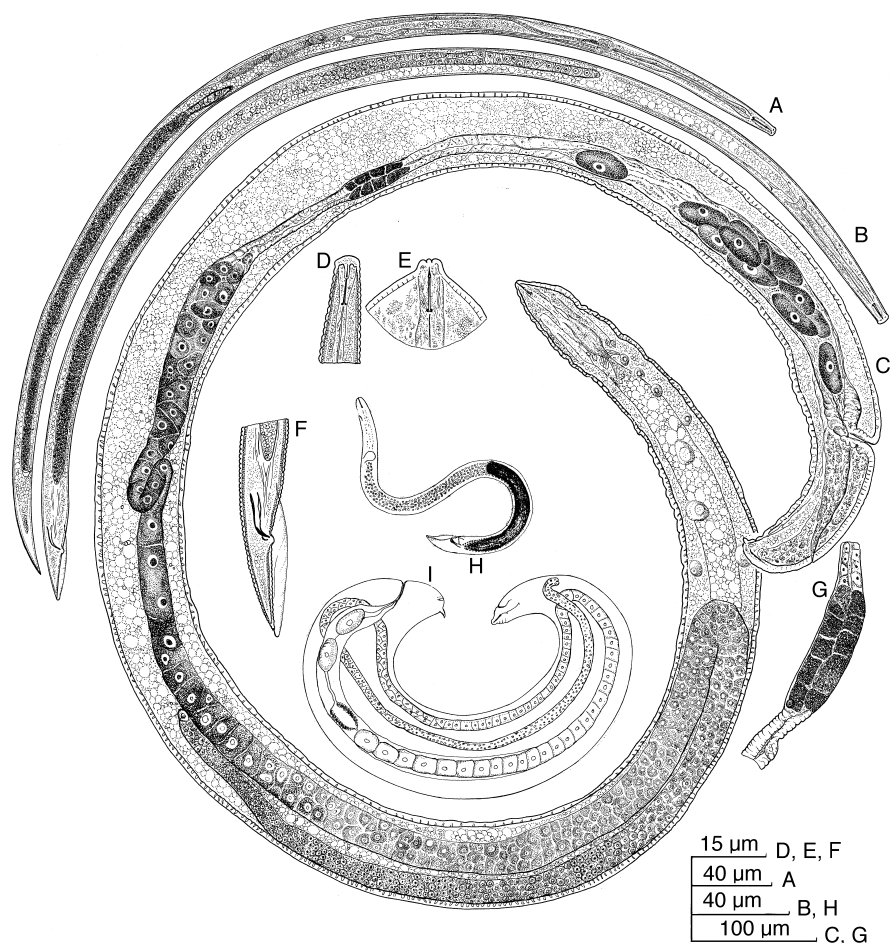
*Aphelenchulus contortus typographi* (Fuchs) Micoletzky, 1925

*Anguillulina contortus typographi* (Fuchs) Baylis & Daubney, 1926

*Aphelenchulus diplogaster* (Fuchs) Filipjev 1934

*Tylenchus contortus cembrae* Fuchs, 1915

*Parasitylenchus contortus cembrae* (Fuchs) Fuchs, 1929



**Fig. 158.** A–G. *Contortylenchus* sp. A. Preadult infective female. B. Free-living male. C, E and G. Parasitic gamogenetic female from haemocoel of wood-boring beetle in Adelaide, Australia. C. Entire female. D and F. Head end and tail end of male, respectively. E. Head end. G. Spermatheca. H and I. *Bovienema tomici* (Bovien). H. Male. I. Parasitic gamogenetic female. (A–G. After Siddiqi (1986). H and I. Redrawn after Bovien (1937).)

#### Other species

*Contortylenchus acuminati* Rühm, 1956

*C. amitini* Rühm, 1956

*C. barberus* (Massey, 1957) Rühm, 1960

syn. *Aphelenchulus barberus* Massey, 1957 (= syn. of *C. brevicomi* for Thong & Webster, 1972)

*C. brevicomi* (Massey, 1957) Rühm, 1960

syn. *Aphelenchulus brevicomi* Massey, 1957



- C. bullus* Massey, 1974  
*C. cribicollis* Rühm, 1956  
*C. cryphali* Rühm, 1956  
     syn. *Contortylenchus cryphali* Rühm, 1954 (= nomen nudum)  
*C. cunicularii* (Fuchs, 1929) Rühm, 1956  
     syn. *Tylenchus contortus cunicularii* Fuchs, 1929  
         *Aphelenchulus cunicularii* (Fuchs) Filipjev, 1934  
         *Parasitylenchus contortus* f. *cunicularii* (Fuchs) W. Schneider, 1939  
*C. elongatus* (Massey, 1960) Nickle, 1963  
     syn. *Aphelenchulus elongatus* Massey, 1960  
*C. genitalicola* Kosaka & Ogura, 1993  
*C. grandicollis* (Massey, 1957) Rühm, 1960  
     syn. *Aphelenchulus grandicollis* Massey, 1957  
*C. laricis* (Fuchs, 1929) Rühm, 1956  
     syn. *Tylenchus contortus laricis* Fuchs, 1929  
         *Aphelenchulus laricis* (Fuchs) Filipjev, 1934  
         *Parasitylenchus contortus* f. *laricis* (Fuchs) W. Schneider, 1939  
*C. orthotomici* Massey, 1974  
*C. proximus* Kakuliya, 1967  
*C. pseudodiplogaster* Slankis, 1969  
*C. rarus* Slankis, 1967  
*C. reversus* (Thorne, 1935) Rühm, 1956  
     syn. *Aphelenchulus reversus* Thorne, 1935  
*C. spirus* (Massey, 1957) Rühm, 1960  
     syn. *Aphelenchulus spirus* Massey, 1957  
*C. terebrans* Massey, 1974

## Remarks

The genus *Contortylenchus* was proposed by Rühm (1956) for the 'contortus' group of species from bark beetles. Some of these species had been previously considered under *Aphelenchus* but, after Rühm (1956), only the type species, *Aphelenchulus mollis* Cobb, 1920, remained in it. Massey's (1957 & 1960) species, described under *Aphelenchulus*, were later transferred to *Contortylenchus*. As discussed under the genus *Aphelenchulus*, further study is needed to clarify its identity.

ETYMOLOGY. From Latin *cum* = with, *torquere* = to twist, and *Tylenchus*.

The type species was found in *Ips typographus* (L.) (type host) and in *I. cembrae* (Heer); up to 50% of the population in Germany was parasitized. *Contortylenchus brevicomi* parasitized 5–38% of the population of *Dendroctonus brevicomis* on Ponderosa pine. *Contortylenchus elongatus* is an effective agent in reducing the brood produced by *Ips confusus* (Le Conte) and *I. lecontei* Swaine. The number of eggs produced by infected beetles was only half as much as by non-infected beetles. Parasitized beetles constructed egg galleries much shorter than those produced by non-infected females (av. 4.5 vs. 7.1 inches). *Contortylenchus elongatus* is known to kill its host and to have effectively reduced the infestation of the beetle in New Mexico, USA (Massey, 1974). *Contortylenchus genitalicola* was cultured on an

unidentified fungus to be used as a biocontrol agent for *Monochamus alternatus* which transmits *Bursaphelenchus xylophilus*, a causal agent of the pine wilt disease (Kosaka & Ogura, 1995). *Contortylenchus* spp. can be used for biocontrol of the bark beetles but this potential has not yet been exploited fully.

### Genus *Bovienema* Nickle, 1963

(Fig. 158, H & I)

#### Diagnosis

Contortylenchinae. **Entomoparasitic female:** Body obese with conoid extremities, dorsally curved with ventral side turned outward, crescent-shaped or in a tight circle, **small** ( $L = 0.44\text{--}0.75\text{ mm}$ ;  $a < 8$ ). Body white with reddish brown patches, behind vulva short, conoid, usually dorsally turned up and with a peg-like process. Cephalic end conoid-rounded. Stylet well developed, with **basal swellings**, not sunken into body,  $9\text{--}14\text{ }\mu\text{m}$  long. **Excretory pore close to stylet base**. Vulva prominent, in a body depression. Ovary long, with one or more flexures, **coiled in anterior and posterior halves of body, often reaching near to vulva**. Uterus, a narrow long tube, with one to three eggs at one time. Oviparous. Eggs hatch in body cavity of host; juveniles penetrate into the intestine, aggregate in rectum and escape via anus. Newly hatched juveniles  $190\text{--}200\text{ }\mu\text{m}$  long; cephalic region continuous; stylet feeble,  $8\text{--}9\text{ }\mu\text{m}$  long; tail short, conoid-rounded. **Males of *B. pityophthori* were found in the host's body cavity** (as compared to *Contortylenchus* spp., in which they always occur in host's galleries). **Partially free-living forms:** **Female:** Small (about  $0.3\text{ mm}$  long), generally shorter and more slender than the male. Cephalic region continuous or slightly expanded. Stylet stronger than that of the male, with basal swellings,  $9\text{--}12\text{ }\mu\text{m}$  long. Orifice of dorsal oesophageal gland less than half stylet length behind stylet base. **Excretory pore opposite orifice of dorsal gland**. Ovary rudimentary, not reaching beyond posterior third of body. Tail conical with a blunt tip, shorter than that of male. **Male:** Stylet feeble, with very slight basal swellings,  $8\text{--}10\text{ }\mu\text{m}$  long. **Excretory pore near stylet base**. Testis outstretched, reaching about middle of body. Spicules small, cephalated, arcuate. Gubernaculum small, trough-shaped. Tail conical, completely enveloped by a bursa.

#### Hosts

Coleoptera: *Cryphalus*, *Ips*, *Pityogenes*, *Pityophthorus*, *Xyleborus*.

#### Type species

*Bovienema tomicis* (Bovien, 1937) Nickle, 1963

syn. *Aphelenchulus tomicis* Bovien, 1937

*Contortylenchus tomicis* (Bovien) Rühm, 1956

#### Other species

*Bovienema cylindricum* (Slankis, 1967) Siddiqi, 1986

syn. *Contortylenchus cylindricus* Slankis, 1967

*B. gifuchsi* Siddiqi, 1986

syn. *Parasitylenchus contortus chalcographi* Fuchs, 1938 nec *Parasitylenchus dispar chalcographi* Fuchs, 1938

*Contortylenchus chalcographi* (Fuchs, 1938) Rühm, 1956  
*B. pityophthori* (Massey, 1974) Siddiqi, 1986  
 syn. *Contortylenchus pityophthori* Massey, 1974

ETYMOLOGY. Commemorative name honouring Prosper Bovien.

The type species was originally found in bark beetle, *Pityogenes bidentatus* (Hbst.), on *Pinus contorta* in Denmark. Bovien (1937) found that, in pine logs, the beetles usually harboured only one gravid *B. tomici* but, when larval beetles appeared in the tunnels, about 60% were found to be infected with females in various stages of gravidity. About 25–30% and 4% of *Pityogenes* beetles were parasitized in Germany and the USA, respectively. Nickle (1963) found on average one female (maximum three) per beetle and stated that the parasitic females were smaller than those of most other allantonematids, which might be due to the small size (2–3 mm long) of the host. The eggs hatch in the host's haemocoel, the juveniles grow and leave the host via the rectum as the fourth stage. In beetle frass, the male fertilizes the female and then it dies. The inseminated preadult female invades the host larva and grows into an adult parasite.

### Genus *Aphelenchulus* Cobb, 1920

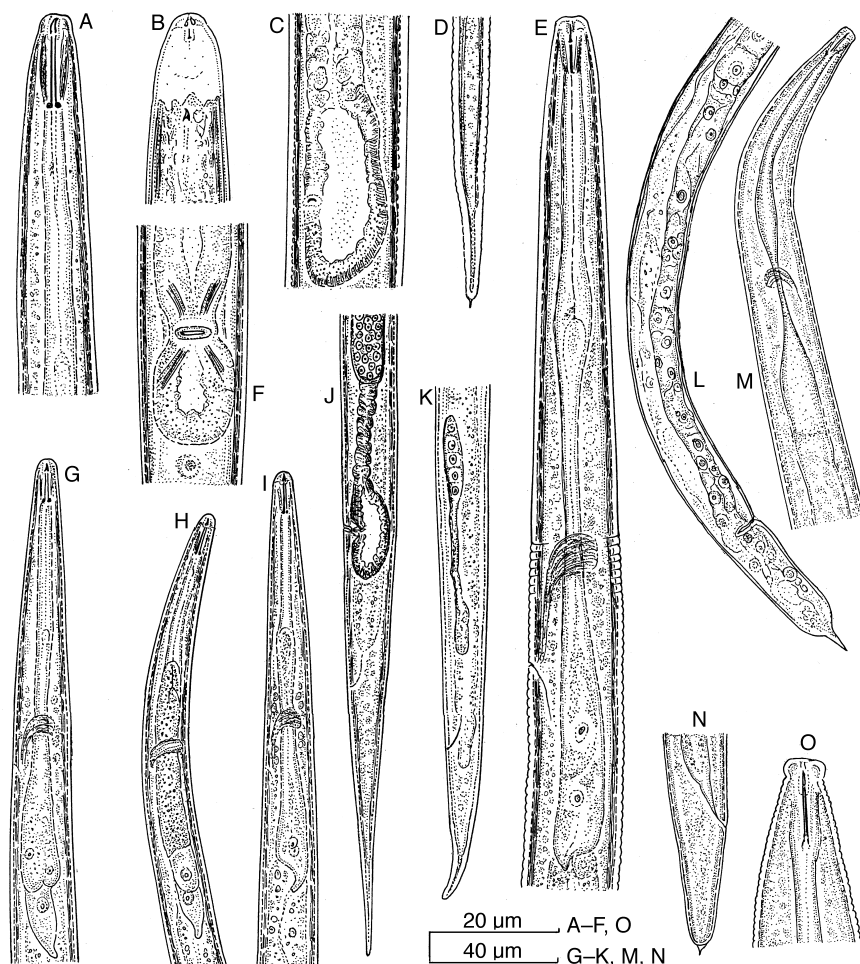
(Fig. 159, L–O)

#### Diagnosis

Contortylenchinae. **Entomoparasitic female: Elongate-obese, tuboid**, arcuate (not clear if dorsally or ventrally), about 2.6 mm long; body-wall firm, not wrinkled. Cephalic region more or less rounded, not overgrown by body expansion. **Stylet knobbed**, in normal position. **Vulva large, conspicuous**, somewhat elevated, especially in front. Uterus straight, with several ellipsoidal eggs,  $40\ \mu\text{m} \times 25\ \mu\text{m}$ , about as long as body width. Ovary reflexed at the tip. Tail end convex-conoid, with a conical spike at tip, not directed dorsally. Oviparous. **Juveniles** (from host): Cuticle finely but distinctly annulated. Lateral fields with 12 incisures, hardly raised, appearing as somatic body muscles. Cephalic region hemispherical to truncate, slightly offset from body by expansion. Stylet slender, about 8–10  $\mu\text{m}$  long; conus about one-fourth of total stylet length; knobs minute, rounded. Orifice of dorsal oesophageal gland close to stylet base. Corpus elongate-cylindroid, with fusiform basal swelling. Isthmus very narrow, enveloped by nerve ring. Basal region of oesophagus and glands obscure. Intestine two-celled in circumference. Rectum less than one anal body width long. Anus distinct. Tail subcylindroid, bluntly obtuse, terminus with a minute mucro. **Partially free-living forms: Male:** Body vermiform, 1 mm long. Lateral field with 12 incisures. Cephalic region and stylet as described for juvenile. Spicules tylenchoid, arcuate, about one and a half times anal body width long. Gubernaculum small, trough-shaped. Tail elongate-conoid, completely enveloped by a bursa. **Female:** Not known.

#### Host

Coleoptera: *Cyllene*.



**Fig. 159.** A–K. *Prothallonema/Pauroidontus* sp. from a fungus on a tree trunk in Luton, England. L–O. *Aphelenchulus mollis* Cobb; L from original sketches by N.A. Cobb; M–O syntypes. A. Anterior end of preadult entomoparasitic female. B and K. Head and tail ends, respectively, of third-stage juvenile. C and F. Vulval regions of preadult females. D and J. Tail ends of preadult females. E and M. Oesophageal regions of juveniles. G–I. Oesophageal regions of preadult females. L. Posterior region of female from haemocoel of *Cyllene picta*. N and O. Tail and head ends, respectively, of juvenile from haemocoel of *Cyllene picta*.

#### Type species

*Aphelenchulus mollis* Cobb, 1920

No other species.

## Remarks

Most nominal species of *Contortylenchus* have been assigned to *Aphelenchulus* Cobb, 1920 at one time or the other and there is a strong possibility that the two genera are synonymous. Nickle (1963) discounted this possibility, arguing that the parasitic female of *Aphelenchulus mollis* Cobb, 1920 is not contorted. Siddiqi's (1986) examination of Cobb's original sketches of *A. mollis*, made available by A.M. Golden, USDA Nematology Laboratory, Beltsville, Maryland, USA, provided a reconstruction of the posterior region of the parasitic female (see Fig. 159, L). Since the vulva is not seen in profile and the body is twisted, it is difficult to know the nature of the body curvature. Cobb's statement that the vulva in this nematode is large and conspicuous supports my reason for assigning *Aphelenchulus* to Contortylenchinae. However, as pointed out by Nickle (1967), there is need to re-collect and re-study this nematode, so as to decide its systematic position. The oesophagus of juveniles in Cobb's original slides showed a very narrow isthmus and a circum-oesophageal nerve ring and, although the basal region was not clear, the similarity with the oesophagus of mycetophagous *Paurodontus* and *Paurodontoides* was apparent.

ETYMOLOGY. Latin diminutive of *Aphelenchus*.

The type species was found parasitizing the thoracic and abdominal haemocoel of an arboricolous beetle, *Cyllene picta* Drury, at Falls Church, Virginia, USA. Three of 14 female and seven of 12 male beetles were found infested; one beetle contained 16,000 juveniles; one to eight mature females per beetle were usually recovered (Cobb, 1920). The two males found by Cobb were in the castings of beetles taken from the infested log.

## SUPERFAMILY IOTONCHIOIDEA GOODEY, 1953 (SIDDIQI, 1986)

## Diagnosis

Hexatyline. Known or suspected parasites of insect haemocoel, with partially free-living stages; **free-living feeding generation present**. In host, **two alternating parasitic generations present**, a primary heterosexual one, in which the female fertilized in the environment invades the host, and a secondary heterosexual or parthenogenetic generation in the host, or (only in *Heteromorphotylenchus*) a parthenogenetic non-feeding female occurring in the environment. Primary heterosexual female is the largest. **Sexual dimorphism in anterior region of partially free-living forms present** or rarely absent. Cuticle finely striated, with lateral fields; deirids near excretory pore or more anterior; phasmids absent. Female cephalic region low or elevated, hexaradiate, **male cephalic region may be tri- or tetralobed and asymmetrical**. Female stylet small or large, with or without basal knobs, **male stylet generally reduced, or absent**. Oesophagus cylindroid or fusiform, **not divisible into distinct corpus, isthmus and basal region, non-muscular; glands elongated extending over intestine mostly dorsally**. Nerve ring apparently circumintestinal. Vulva posterior, may be over two vulval body widths anterior to anus. Postvulval uterine sac absent. **Spicules large, L-shaped** in type family, in other family may be small, arcuate. Gubernaculum present or absent.

## Type family

Iotonchiidae Goodey, 1953 (Skarbilovich, 1959)

## Other family

Parasitylenchidae Siddiqi, 1986

**Key to families of Iotonchioidea**

1. Marked sexual dimorphism in anterior region present; vulva more than two body widths from anus; spicules robust, angular ..... **Iotonchiidae**  
 Marked sexual dimorphism in anterior region absent; vulva less than two body widths from anus; spicules neither robust nor angular ..... **Parasitylenchidae**

**Family Iotonchiidae Goodey, 1953 (Skarbilovich, 1959)**

## Diagnosis

Iotonchioidea. Two types of female occur in host's body cavity, a primary heterosexual female curving ventrally and spirally and having vulva at more than two body widths from anus, and a secondary parthenogenetic female. Alternation of heterosexual and parthenogenetic generations present. **Partially free-living forms with marked sexual dimorphism in anterior region**, in which male oesophagus is degenerate and stylet degenerate or absent. Male cephalic region tri- or tetralobed, usually asymmetrical. Female stylet generally over 18  $\mu\text{m}$  long, usually without basal knobs, indistinct basal knobs or thickenings may be present. Excretory pore opposite or behind nerve ring. **Vulva more than two body widths in front of anus**, with or without anterior lip flap. A ventromedian body pore behind vulva present or absent. Vagina strongly muscular. No postvulval uterine sac. Tails generally elongate-conoid, or filiform. **Spicules robust, angular, L-shaped or of an aberrant form, in two parts, proximal part broad and cephalated, distal part slender, with rounded or spined tip**. Large postanal genital papillae may be present (*Fungiotonchium*). Bursa small, adanal, or large, completely enveloping tail.

## Type subfamily

Iotonchiinae Goodey, 1953

No other subfamily.

**Subfamily Iotonchiinae Goodey, 1953**

**syn. Skarbilovinematinae Chizhov & Zakharenkova, 1991**

## Diagnosis

Iotonchiidae. With characters of the family.

## Type genus

*Iotonchium* Cobb, 1920

## Other genera

*Fungiotonchium* Siddiqi, 1986*Paraiontonchium* Slobodyanyuk, 1975*Skarbilovinema* Chizhov & Zakharenkova, 1991**Key to genera of Iotonchiinae**

(based on free-living entomoparasitic forms)

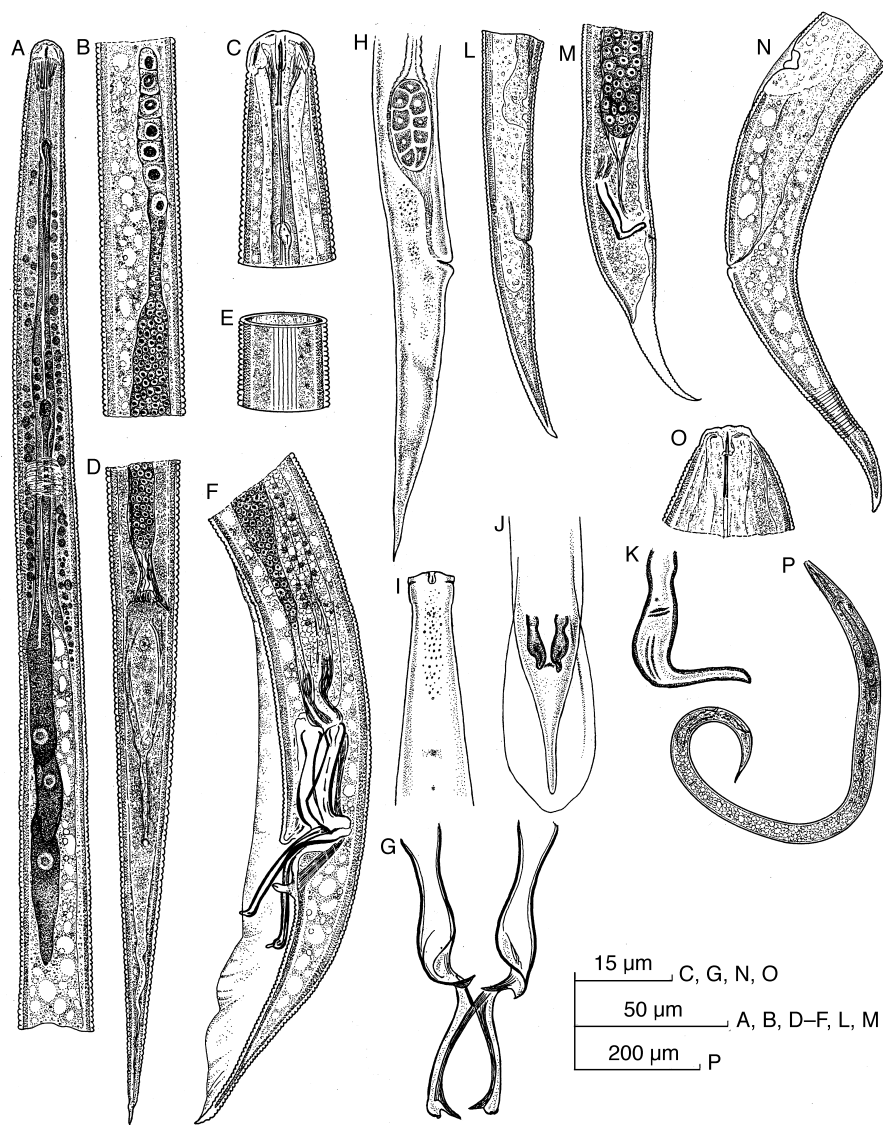
1. Vulva covered by anterior lip flap; spicules cylindroid, distally bearing an extremely slender extension that ends in spine or notch ..... 2  
    Vulva not covered by anterior lip flap; spicules L-shaped, distal portion not extremely slender ..... 3
2. Bursa covering entire tail ..... *Fungiotonchium*  
    Bursa covering only two-thirds of tail ..... *Skarbilovinema*
3. Marked sexual dimorphism in anterior region present, male stylet degenerate or absent; bursa large, enveloping tail ..... *Iotonchium*  
    Marked sexual dimorphism in anterior region absent, male stylet normal; bursa small, adanal ..... *Paraiontonchium*

**Genus *Iotonchium* Cobb, 1920****syn. *Anguillulina* (*Iotonchium* Cobb, 1920) (Schneider, 1939)**

(Fig. 160, H–P)

## Diagnosis

Iotonchiinae. Adult parasitic female and insect host not known for type species. Body tuboid, ventrally arcuate. Stylet present but indistinct. Tail cylindroid. Oviparous. **Partially free-living forms:** associated with fungi. **Male:** Straight to ventrally arcuate upon relaxation, 0.54–0.68 mm long,  $a = 19\text{--}23$  in type species. Cuticle finely annulated. Lateral field about one-sixth body width, with ten distinct incisures. **Cephalic region dorsoventrally flattened, asymmetrical, trilobed, not bent to the side. Stylet degenerate or absent,** oesophagus degenerate. Deirids near excretory pore behind nerve ring. Testis single, outstretched, reaching nerve ring; vas deferens packed with moderately large sperm, **spicules robust, large, L-shaped,** distal arm not attenuated, tip not spined in type species. Gubernaculum absent. Tail conoid. **Bursa large, arising well anterior to spicule head, enveloping tail. Postanal ventral papillae absent.** Preadult male juvenile is precocious, having fully developed testis and spicules but no bursa. The asymmetry of the cephalic region and degeneration of the stylet and oesophagus occur at the final moult. **Preadult entomoparasitic female** (not known for type species): Partially free-living, developing in and parasitizing insect haemocoel. Body 0.97–1.5 mm long;  $a = 32\text{--}85$ . Stylet 10–23  $\mu\text{m}$  long, basal thickenings asymmetrical. Orifice of dorsal oesophageal gland about one stylet length behind stylet base. Oesophagus cylindroid, non-muscular. Oesophageal glands elongated, on dorsal side of intestine, nuclei of equal size, DN behind SVN. Vulva at 81–88% of body length, **lacking anterior lip flap.** Prodelphic. No postvulval uterine sac. Gonad immature. Ovary with five or six cells in a row, not reaching midbody region. Tail elongate-conoid. **Gravid free-living female** described for type species by Bütschli (1876). Body 0.8–1.8 mm long. Cuticle



**Fig. 160.** A–D. *Fungiotonchium bifurcatum* (Goodey), paratypes. E–G. *Fungiotonchium fungorum* (Bütschli). H–K. *Iotonchium imperfectum* (Bütschli). L, M and P. *Iotonchium cephalostrictum* Meyl (Meyl's original specimens at Rothamsted). N and O. *Iotonchium mycophilum* Meyl (Meyl's original specimen). A, C and O. Anterior ends of preadult (?) entomoparasitic females. B and D. Ovary and tail end (ventral view) of preadult female, respectively. E. Lateral field. F and J. Tail ends of males. G. Spicules in ventral view. H. Tail end of gravid female. I. Head end of male. K. Spicule in lateral view. L and N. Tail ends of third-stage female juveniles. M. Tail end of fourth-stage male juvenile. P. Third-stage female juvenile. (H–K. Redrawn after Bütschli (1876). Remainder after Siddiqi (1986).)



finely striated. Cephalic region swollen. Stylet distinct, 8  $\mu\text{m}$  long. Vulva at 88–89% of body length. Ovary reaching oesophagus. Only one egg in uterus at one time. No postvulval uterine sac. Tail elongate-conoid with finely rounded terminus, about four and a half times anal body width long.

#### Type species

*Iotonchium imperfectum* (Bütschli, 1876) Cobb, 1920

syn. *Tylenchus imperfectus* Bütschli, 1876

*Anguillulina (Iotonchium) imperfecta* (Bütschli) Schneider, 1939

#### Other species

*Iotonchium cateniforme* Tsuda & Futai, 1999

*I. cephalostrictum* Meyl, 1954

#### Species incerta sedis

*Iotonchium mycophilum* Meyl, 1954

#### Nomen nudum

*Iotonchium sabulosum* Izatullaeva, 1967

#### Remarks

Cobb (1920) proposed the genus *Iotonchium* with *Iotonchium imperfectum* (= *Tylenchus imperfectus* Bütschli, 1876) as type and only species of the genus. Bütschli (1876) gave measurements of the female but not of the male. The female was 1.8 mm long,  $a = 23.3$ ,  $V = 89.4$ ; the uterus had a single egg at one time and the eggs measured 60–80  $\mu\text{m}$  long. Bütschli (1876) and Cobb (1920) described the female of the species first, and gave the male characters later. This shows that the species was based on the female and not on the male. Perhaps on the basis of the female, Filipjev & Schuurmans Stekhoven (1941) synonymized *Hexatyclus* Goodey, 1926 and *Neotylenchus* Steiner, 1931 with *Iotonchium*.

The genus *Iotonchium* was mainly recognized on male characteristics, especially the shape of the spicules, as the studies made by Meyl (1961), T. Goodey (1953) and J.B. Goodey (1956) indicated. T. Goodey (1953) discussed the taxonomy of *Iotonchium* and argued that the gravid female of *Tylenchus imperfectus* described by Bütschli (1876) could not be the true female corresponding to the male as it was figured with a segmented egg in the uterus (see Fig. 160, H). His study showed that the females associated with *Iotonchium*-type males had immature ovaries and were perhaps the preadult stage of a parasite of the insect haemocoel. He, therefore, disregarded the female and re-diagnosed *Iotonchium* with male characters, giving them precedence over the female characters.

As early as 1936, Filipjev thought that *Iotonchium* and *Neotylenchus* (= *Hexatyclus*) might be synonymous, and Filipjev & Schuurmans Stekhoven (1941) formally synonymized both *Neotylenchus* and *Hexatyclus* with *Iotonchium*. However, the species included by these authors in the genus *Iotonchium* are now assigned to three or four different genera. The male characters of *I. imperfectum* are sufficient to characterize not only the species but also the genus *Iotonchium*, of which it is the type species. Since a holotype was not designated for this species and the prevailing

concept of the genus *Iotonchium* was based primarily on the male character and to preserve the stability of nomenclature, the male of *T. imperfectus*, whose tail is sketched by Bütschli (1876) in his figure 7a of plate 22, designated by Siddiqi (1986) as lectotype, under the provisions of the ICZN Article 74(b) and (c). This established the type species of *Iotonchium*, which is the type genus of the subfamily Iotonchiinae T. Goodey, 1953. Siddiqi (1986) pointed out that the gravid female of *Tylenchus imperfectus* described by Bütschli (1876) could be the self-perpetuating free-living stage of the species.

A similar female, which is the free-living mycetophagous form, and its entomoparasitic stage were described by Poinar (1991) for *Iotonchium californicum* Poinar (now in *Fungiotonchium*) and by Tsuda & Futai (1999) for *Iotonchium cateniforme*. These species parasitize the fungus gnat and their free-living stages feed on mushrooms (Agaricales). Poinar (1991) also reported a similar form fossilized along with a fungus gnat of the family Mycetophilidae in amber from Dominican Republic and concluded that the fossil evidence suggested that the nematode–gnat association had existed for some 25–40 million years.

ETYMOLOGY. From Greek alphabet *Iota* (= small), and *onchium* = tooth (stylet).

The type species was found in decaying fungi ('faulen Pilze') in Germany.

### Genus *Fungiotonchium* Siddiqi, 1986

(Fig. 160, A–G)

#### Diagnosis

Iotonchiinae. Adult entomoparasitic female and insect host not known. **Partially free-living forms:** In fungi or associated soil. **Male:** About 1–2 mm long, being shorter than female. Cephalic region asymmetrical; dorsoventrally flattened, trilobed; cephalic papillae raised; cephalic end of body directed slightly ventrally. Stylet degenerate or absent. Oesophagus reduced. Testis single, outstretched almost to nerve ring, vas deferens packed with minute, rounded sperm. Tail elongate-conoid, completely enveloped by a large bursa that arises well anterior to the spicule head. **Spicules large, robust, broadly cylindroid, cephalated, distally bearing extremely slender extension that ends in a spine or notch and projects out from cloacal aperture, being directed posteriorly.** Gubernaculum absent. Cloacal aperture partially covered by anterior flap. **A pair of large ventral genital papillae present behind cloacal aperture.** **Female:** Partially free-living, preadult, suspected of parasitizing insect haemocoel. Body slender, 1.2–3.7 mm long, almost straight when relaxed. Cuticle finely striated. Lateral field with four incisures; deirids distinct, near hemizonid and excretory pore, behind nerve ring. Cephalic region continuous or offset by expansion, elevated, **dome-shaped**, smoothly rounded; **framework high arched**; oral opening a central depression; sensilla not raised above the cephalic contour. Stylet slender, 15–20 µm long; conus tubular with distinct lumen, about 5 µm long; basal knobs very minute or absent. Oesophago-intestinal junction anterior to nerve ring; glands elongated, extending over intestine dorsally. **Vulva overhung by a large anterior lip flap**, at 80–85% of body length, associated with a **medioventral papillae** about one body width behind it. Vagina thick-walled, muscu-

lar, tuboid, directed forward. No postvulval uterine sac. Uterus elongate, crowded with sperm and extending to midbody region when impregnated. Ovary immature, outstretched, with oocytes in one or two rows. Female tail elongate-conoid, sharply pointed or terminally filiform.

#### Type species

*Fungiotonchium bifurcatum* (T. Goodey, 1953) Siddiqi, 1986  
syn. *Iotonchium bifurcatum* T. Goodey, 1953

#### Other species

*Fungiotonchium californicum* (Poinar, 1991) comb. n.  
syn. *Iotonchium californicum* Poinar, 1991  
*F. fungorum* (Bütschli, 1873) Siddiqi, 1986  
syn. *Tylenchus fungorus* Bütschli, 1873  
*Hexatyclus fungorus* (Bütschli) T. Goodey, 1932  
*Neotylenchus fungorus* (Bütschli) Filipjev, 1936  
*Anguillulina fungora* (Bütschli) Schneider, 1939  
*Iotonchium fungorum* (Bütschli) Filipjev & Schuurmans Stekhoven, 1941  
(T. Goodey (1953) also proposed this combination)  
*F. macrospiculatum* (Meyl, 1954) Siddiqi, 1986  
syn. *Hexatyclus macrospiculatus* Meyl, 1954  
*Iotonchium macrospiculatum* (Meyl) J.B. Goodey, 1956

ETYMOLOGY. Prefix from fungus, and *Iotonchium*.

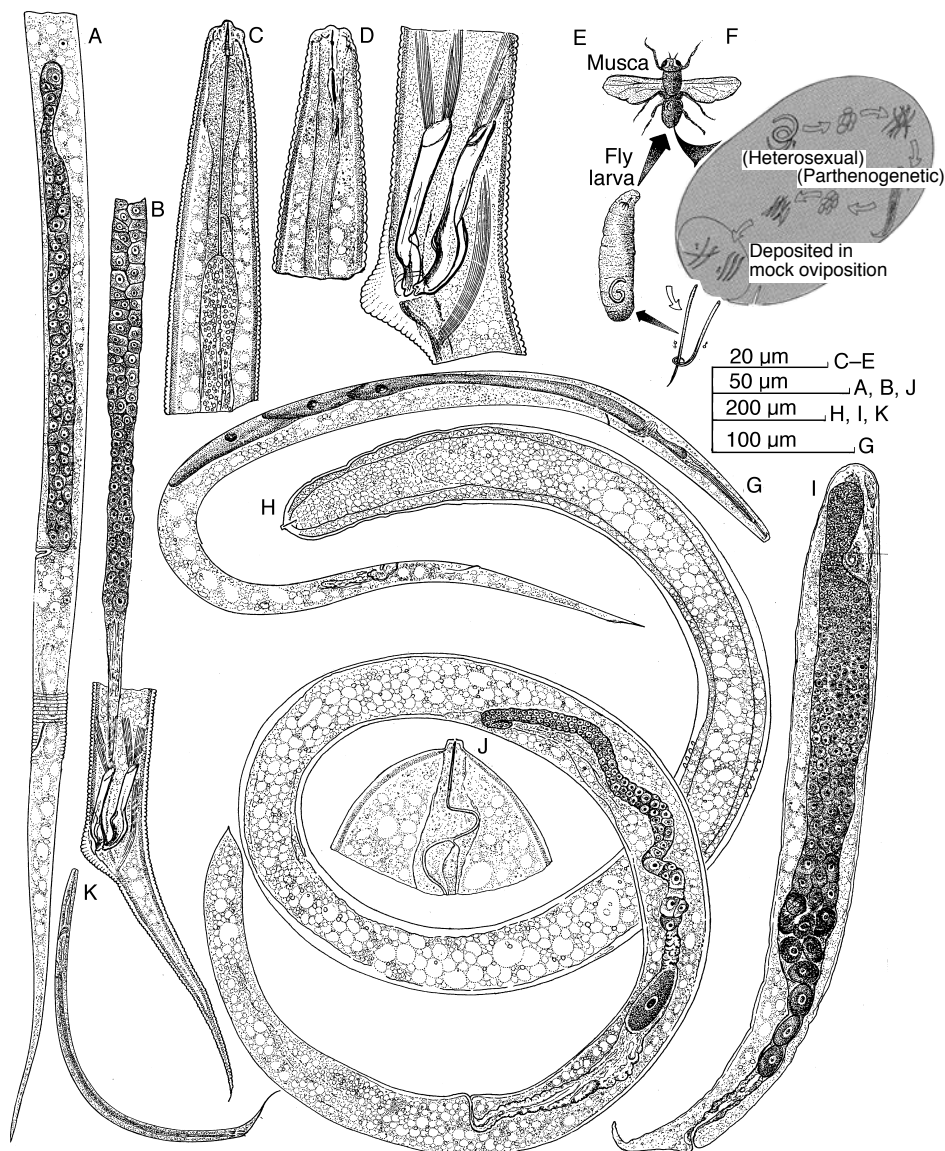
The type species was found in rotting specimens of a basidiomycetous fungus (*Entoloma rhodipolium*) in England. *Fungiotonchium fungorum* was found in Germany in decaying fungi. T. Goodey (1953) found it in England on basidiomycetous fungi, *Entoloma rhodipolium*, *Pleurotus corticatus* and *P. ostreatus*. *F. californicum* is a parasite of fungus gnat, *Mycetophila fungorum*.

### Genus *Paraiotonchium* Slobodyanyuk, 1975

(Fig. 161)

#### Diagnosis

Iotonchiinae. **Two types of adult female in insect host**, one primary heterosexual, which is impregnated in the environment, another secondary parthenogenetic. **A parthenogenetic cycle in host present. Entomoparasitic forms: Primary heterosexual female:** In insect haemocoel. Body elongate-saccate, vermiform, **spirally coiled** when relaxed, 2.8–7.6  $\mu\text{m}$  long;  $a = 19\text{--}45$  in type species. Stylet with smooth base, in normal position. Oesophagus degenerate. Vulva over two body widths anterior to anus, at about 78–84% of body length. Postvulval uterine sac absent. Uterus with one or two eggs at one time. Ovary short, not reflexed, extends to less than half of body length. Tail elongate-cylindroid, abruptly narrowed at terminus to form a spike. Total eggs laid about 24. Eggs hatch and develop into adult parthenogenetic females in the haemolymph. **Secondary parthenogenetic female:** Body cigar-shaped, with posterior end dorsally bent, smaller and more robust



**Fig. 161.** *Paraiontonchium autumnale* (Nickle). A and C. Posterior and anterior region, respectively, of fertilized preadult infective female. B and D. Posterior and anterior region, respectively, of free-living male. E. Spicular region. F. Life cycle. G. Preadult infective female. H and I. Mature gametogenetic female and secondary parthenogenetic female, respectively, from the haemocoel of *Musca autumnalis* collected in New York, USA. J. Head end of mature gametogenetic female. K. Free-living male collected in Montreal, Canada. (After Siddiqi, 1986)

( $L = 1.4\text{--}1.7$  mm;  $a = 9\text{--}14$ ) than in the primary female. Stylet  $14\text{--}17$   $\mu\text{m}$  long, without knobs. Oesophagus degenerate. Vulva near anus. Ovary large, extends into stylet region, oocytes arranged about a rachis. No postvulval uterine sac. Uterus with several eggs at one time. Tail elongate-conoid, ventrally arcuate, with a small rounded tip. Oviparous, lays several hundred eggs in haemolymph, where they hatch to develop into small (1 mm long) female and male juveniles, which penetrate the insect ovary and are laid *en masse* in mock oviposition in dung manure of cattle and horses, where they develop and mate and the fertilized female seeks out and penetrates a host's larva. **Partially free-living heterosexual forms:** Found in insect ovaries and in the environment (dung or fungi). **Female:** Slender, vermiform,  $0.47\text{--}1$  mm long, almost straight or bow-shaped when relaxed. Cephalic region continuous. Stylet well developed, with dorsally oblique aperture, **lacking basal knobs or swellings**,  $13\text{--}27$   $\mu\text{m}$  long; **orifice of dorsal gland almost a stylet length behind stylet base**. Oesophageal glands extend to midbody. Oesophagus cylindrical, non-muscular. Excretory pore behind nerve ring; duct sclerotized. Ovary rudimentary. Uterus elongate, packed with **moderately large sperm**. Vulva at some distance from anus, lips not protuberant. Tail elongate, regularly tapering, conical or filiform. No caudal pores or phasmids. **Male:** Body dorsally bent behind anus. Stylet  $8\text{--}19$   $\mu\text{m}$  long. Tail as in female. **Bursa adanal, rudimentary** (? absent in *P. nicholasi*). Testis outstretched; sperm moderately large. **Spicules large** (about  $40\text{--}50$   $\mu\text{m}$  long), **L-shaped, with a scoop-like distal portion**. **Gubernaculum absent**.

#### Hosts

Diptera: *Musca*, *Stomoxys*.

#### Type species

*Paraiontonchium autumnale* (Nickle, 1967) Slobodyanyuk, 1975  
syn. *Heterotylenchus autumnalis* Nickle, 1967

#### Other species

*Paraiontonchium crassirostris* (Yatham & Rao, 1981) Siddiqi, 1986  
syn. *Heterotylenchus crassirostris* Yatham & Rao, 1981  
*P. muscadomesticae* Coler & Nguyen, 1994  
*P. nicholasi* Slobodyanyuk, 1975  
syn. *Heterotylenchus autumnalis* apud Nicholas & Hughes, 1970 nec Nickle, 1967  
*P. osiris* Slobodyanyuk, 1976  
*P. xanthomelas* (Reddy & Rao, 1988) comb. n.  
syn. *Heterotylenchus xanthomelas* Reddy & Rao, 1988

ETYMOLOGY. From Greek *para* = beside, and *Iotonchium*.

*Paraiontonchium autumnale*, *P. nicholasi* and *P. osiris* parasitize haemocoels of *Musca autumnalis* De Geer, *M. vetustissima* Walker and *M. osiris* Wiedemann, respectively. *Paraiontonchium crassirostris* parasitizes *Musca crassirostris* Stein and *Stomoxys calcitrans* L. in Hyderabad, India, where, in the monsoon period (July–September), the percentage of infection reaches up to 20. The nematode juveniles feed on oocytes, and

the host's eggs are not seen in the ovarioles. The fly deposits juvenile nematodes through its ovipositor on the fresh cow-dung in the pasture, where they grow, mate and the infective female attacks the host's larva.

In Nebraska, USA, 10–60% of the population of *Musca autumnalis*, the facefly of cattle and horses, is infected by *P. autumnale*; both heterosexual and parthenogenetic females were recovered from hibernating flies (Nickle, 1967). The eggs of heterosexual females are brown, those of parthenogenetic females are white. At the emergence of the adult fly, the nematode's stage is the heterosexual female; parthenogenetic females appear in 3 days and, after 7 days, all stages of nematodes are present in the haemocoel. In 9 days the nematode's invade the host's ovaries which cease to develop. The infected females do not produce eggs; only nematode juveniles present in the ovarioles are deposited in bovine dung during mock oviposition. Infected male flies have normal testes and do not transmit infection. The nematode significantly reduces the population of facefly in Missouri, USA. Sterility of the facefly may be caused by a toxic substance produced by the parasite, or by the destruction of the corpora alata. Stoffolano (1967) demonstrated that the life cycle of the parasite and its host are synchronized.

Nickle (1967) reported the mass rearing of the parasite on flies and its successful introduction as a biocontrol agent in Montana and California, USA, with the result that 25–50% of faceflies were sterilized. However, Geden & Stoffolano (1984) cautioned that in any biocontrol programme it was essential to evaluate the potential of a host to respond to the parasite, since the parasite may be encapsulated, melanized and rendered ineffective by the host's defence reaction. *Paraiontonchium autumnale* was also found parasitizing *M. autumnalis* in the Crimea and *Musca* spp. in Czechoslovakia. *Paraiontonchium osiris* was found in *Musca osiris* in Turkmenia.

*Paraiontonchium muscadomesticae* has biocontrol potential against the house fly. It infected *Musca domestica* eggs and caused heavy mortality. Infected flies contained 12,000–45,000 gamogenetic nematodes 10–14 days after fly emergence and there was no difference in the infection rate between the sexes of flies. In the rearing medium, nematodes persisted for 3–5 days after deposition, but not after 7 or 10 days. Infection of flies halved their lifespan (Geden, 1997).

### Genus *Skarbilovinema* Chizhov & Zakharenkova, 1991

(Fig. 162)

#### Diagnosis

Iotonchiinae. Only heterosexual stages known. **Primary heterosexual female:** Develops from preadult fertilized female that invades host's larva or pupa, and attains full maturity in adult host. Obese, **elongate-tuboid with rounded ends, 3–16 (8) mm long**, old females yellow in colour. Cuticle reduced, body-wall covered with numerous interwoven cytoplasmic hypodermal microvilli for food uptake. Intestine narrow, without lumen. Genital branch reflexed several times, almost filling body cavity. Stylet 22–28 µm long. Vulva at 96–99% of body length. Anus present. **Viviparous. Juveniles develop into bisexual stages. Fertilized infective-stage female:** Body elongate-slender ( $L = 2.87\text{--}3.34\text{ mm}$ ;  $a = 72\text{--}104$ ). Cephalic region offset from body. Stylet without basal knobs. Oesophagus cylindroid, with sclerotized lumen. Three oesophageal glands well developed, occupying 30–40% of body

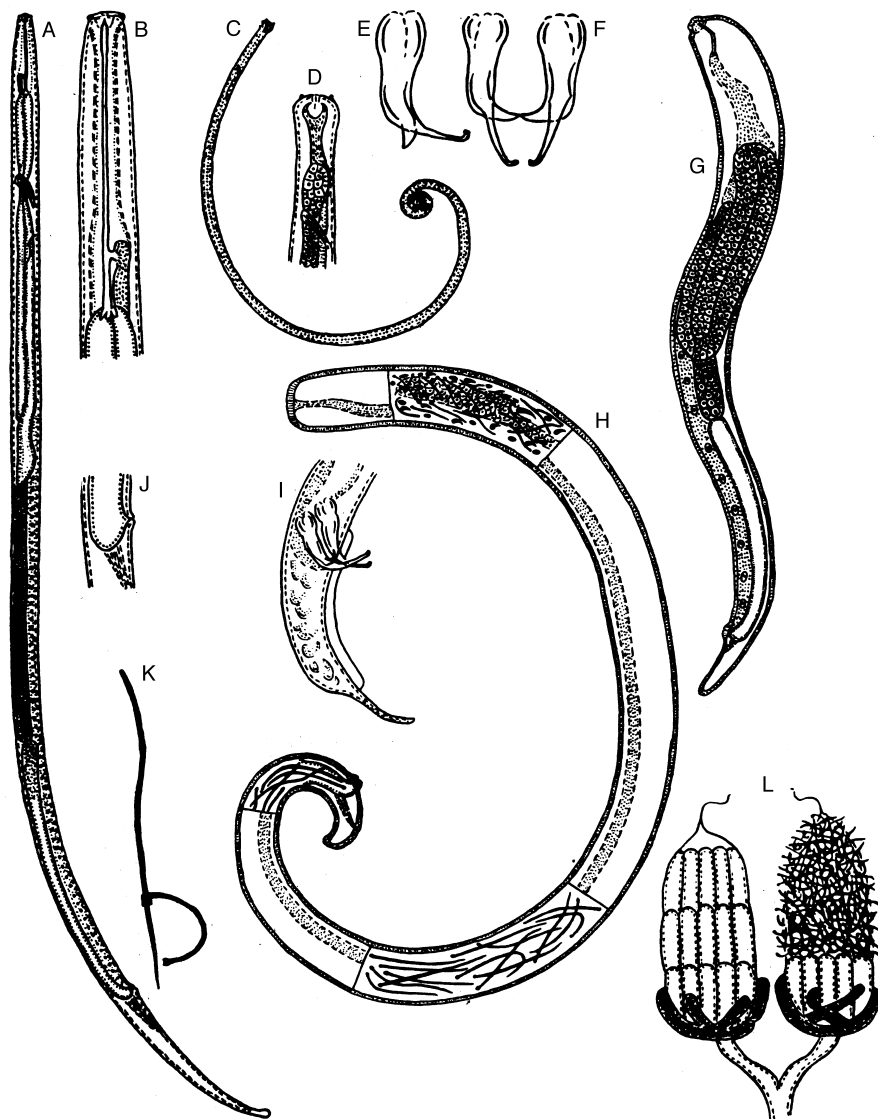


Fig. 162. *Skarbilovinema laumondi* Chizhov & Zakharenkova. A. Fertilized preadult infective female. B. Anterior region of infective female. C. Male. D. Anterior end of male. E. Spicule, lateral view. F. Spicules, ventral view. G and H. Young and old parasitic females, respectively. I. Posterior region of male. J. Vulva region of infective female. K. Female and male, in copulation. L. Infection of host's ovary. (After Chizhov & Zakharenkova, 1991.)

length. Vulva at 92–93% of body length. Genital branch occupying about 60% of body length, well differentiated into ovary and uterus; latter filled with small-sized sperm. **Vulva lips prominent.** **Male:** Cephalic region pin-head-like. Stylet and

oesophagus degenerate. Sperm small, rounded, packing the gonoduct. Spicules huge, with widened proximal and narrow distal regions. Gubernaculum absent. **Bursa narrow, covers about two-thirds of tail.** Tail curved ventrally.

#### Hosts

Diptera: *Helophilus*, *Eristalis*.

#### Type species

*Skarbilovinema laumondi* Chizhov & Zakharenkova, 1991

#### Other species

*Skarbilovinema lyoni* Chizhov & Zakharenkova, 1991

ETYMOLOGY. Patronym honouring T.S. Skarbilovich.

The type species parasitizes flies of the family Syrphidae, belonging to three species: *Helophilus pendulus*, *H. trivittatus* and *Helophilus* sp. in Russia, in Moscow, Jaroslavl, Vladimir, Kalinin and Vologda regions, and also in West Caucasus. *Skarbilovinema lyoni* parasitizes *Eristalis arbustorum* and *E. horticola* in Moscow, Jaroslavl, Vladimir, Tver, Kaluga and Tula regions of Russia.

## Family Parasitylenchidae Siddiqi, 1986

#### Diagnosis

Iotonchioidea. Two or three types of adult present in host body cavity, **primary heterosexual generation alternating with a secondary heterosexual or parthenogenetic generation**; rarely non-feeding parthenogenetic female of the secondary generation occurs in the environment (*Heteromorphotylenchus*), or not known (*Spilotylenchus*). Primary heterosexual female dorsally or ventrally curved, but not curving spirally, when relaxed. Female stylet generally under 18 µm long, with basal thickenings or **knobbed**. Orifice of dorsal gland close to or further behind stylet base. Excretory pore generally anteriorly placed. **Vulva less than two body widths from anus**, lips not modified; no ventral body pore near vulva. Vagina poorly muscular. Postvulval uterine sac absent. Female tail short, subcylindroid or conoid. Male may occur in host's body cavity (*Parasitylenchus*, *Kurochkintylenchus*). **Spicules slender, simple, ventrally arcuate**, about 20 µm or less long (except 27–30 µm long in *Parasitylenchus macrobursatus*). Bursa enveloping tail, or absent (*Heterotylenchus*). Gubernaculum present or absent.

#### Type subfamily

Parasitylenchinae Siddiqi, 1986

#### Other subfamily

Heterotylenchinae Siddiqi, 1986

Heteromorphotylenchinae Siddiqi, 1986



Kurochkinitylenchinae Slobodyanyuk, 1999  
 Spilotylenchinae Slobodyanyuk, 1999

### Key to subfamilies of Parasitylenchidae

1. With two types of alternating heterosexual generation; copulation takes place in host's body cavity ..... 2  
 Only one type of heterosexual generation; copulation does not take place in host's body cavity ..... 3
2. Parasitic females dorsally curved; parasites of Siphonaptera ..... **Kurochkinitylenchinae**  
 Parasitic females ventrally curved; parasites of Diptera and Coleoptera ..... **Parasitylenchinae**
3. Parthenogenetic non-feeding female and its eggs found in environment ..... **Heteromorphotylenchinae**  
 Parthenogenetic parasitic female and its eggs found in host's coelom ..... 4
4. Parasitic females usually dorsally curved; excretory pore generally anterior to nerve ring; parasites of Siphonaptera ..... **Spilotylenchinae**  
 Parasitic females not dorsally curved; excretory pore generally posterior to nerve ring; parasites of Diptera and Coleoptera ..... **Heterotylenchina**

### Subfamily Parasitylenchinae Siddiqi, 1986 (Parasitylenchinae Rühm, 1956 = nomen nudum)

#### Diagnosis

Parasitylenchidae. Five distinct adult forms, **with two types of alternating heterosexual generation**. Three types of adult in host's body cavity – primary heterosexual female, secondary heterosexual female, and male of secondary heterosexual generation. Parasitic females straight or ventrally curved when relaxed. **Copulation takes place in host's body cavity**. Spermatozoa small-sized. Gubernaculum and bursa may be absent. Excretory pore usually located behind nerve ring. Primary heterosexual female sausage- or spindle-shaped, produces heterosexual forms which multiply in the host's body cavity. The latter produce male and female juveniles that leave host for further development and copulation in the environment. **Parasites of Diptera and Coleoptera**.

#### Type genus

*Parasitylenchus* Micoletzky, 1922  
 No other genus.

**Genus *Parasitylenchus* Micoletzky, 1922**syn. *Parasitylenchus* (*Parasitylenchus* Wachek, 1955)*Polymorphotylenchus* Rühm, 1956 (= objective syn.)*Polymorphotylenchus* (*Thylakolenchus* Rühm, 1956)*Vasotylenchus* Slankis, 1967

(Fig. 155, H–P)

**Diagnosis**

*Parasitylenchinae*. **With three types of adult in host** – primary heterosexual female, secondary heterosexual female, and male. **Entomoparasitic forms: Secondary heterosexual forms copulate in host's haemocoel. Primary large heterosexual female:** Develops from preadult fertilized female that invades host's larva or pupa, and attains full maturity in adult host. Obese, **sausage-shaped, curving ventrally**, with round, wrinkled ends, about 0.8–1.3 mm long, milky white to transparent, often with red-brown or dark brown spots of metabolic products. Cephalic region usually overgrown by body expansion. Stylet about 8–11  $\mu\text{m}$  long, with **minute basal knobs**. Vulva subterminal. Uterus filling most of body cavity, with ovary convoluted in anterior region. Oviparous or ovoviviparous. Eggs about 60  $\mu\text{m}$   $\times$  20  $\mu\text{m}$ . **Juveniles develop into bisexual forms in host's body cavity. Secondary small heterosexual female:** About 0.3–0.7 mm long, less obese and in larger numbers than primary females. White or yellowish-brown. Stylet similar to that in primary female. **Excretory pore near stylet base** (except *P. diplogenus* and *P. nearcticus*, in which it is behind nerve ring). Ovary outstretched or with one or more flexures. Tail conoid or obtusely round. **Male: In host's body cavity.** Smaller than secondary heterosexual female but not obese; as numerous as secondary heterosexual females. Cephalic region continuous. Excretory pore near stylet base (posterior to nerve ring in *P. nearcticus*). Stylet reduced (not required for feeding), with or without basal knobs, 8–10  $\mu\text{m}$  long. Testis outstretched. Tail tapering to a rounded tip. Bursa absent in type species, a low bursa enveloping tail may be present. Spicules cephalated, arcuate, small (10–16  $\mu\text{m}$ ). Gubernaculum present (except in *P. diplogenus*). **Partially free-living forms:** Juveniles of *P. diplogenus* destined for free life have their third moult in host's gonads, and the fourth in the environment, where copulation takes place. Infective females of *P. nearcticus* have strong stylet lacking knobs and enlarged oesophageal gland.

**Hosts**Diptera: *Drosophila*.Coleoptera: *Conophthorus*, *Ips*, *Pityokteines*, *Hormonia*.**Type species***Parasitylenchus dispar* (Fuchs, 1915) Micoletzky, 1922syn. *Tylenchus dispar typographi* Fuchs, 1915 (*T. dispar typographi* Fuchs, 1914 = nomen nudum)*Aphelenchulus dispar typographi* (Fuchs) Micoletzky, 1925*Anguillulina dispar typographi* (Fuchs) Baylis & Daubney, 1926*Polymorphotylenchus* (*Polymorphotylenchus*) *typographi* (Fuchs) Rühm, 1956

## Other species

- Parasitylenchus aculeatus* Slankis, 1972  
*P. coccinellinae* Iperti & Waerebeke, 1968  
*P. curvidentis* (Fuchs, 1914) Micoletzky, 1922  
     syn. *Tylenchus dispar curvidentis* Fuchs, 1914  
         *Aphelenchulus dispar curvidentis* (Fuchs) Micoletzky, 1925  
         *Anguillulina dispar curvidentis* (Fuchs) Baylis & Daubney, 1926  
         *Polymorphotylenchus* (*Thylakolenchus*) *curvidentis* (Fuchs) Rühm, 1956  
*P. diplogenus* Welch, 1959  
     syn. *Polymorphotylenchus diplogenus* (Welch) Baker, 1962  
*P. klimenkorum* Korentchenko, 1987  
*P. macrobursatus* Blinova & Gurando, 1977  
*P. nearcticus* Poinar, Jaenike & Dombeck, 1997  
*P. orthotomici* Ho, Kaya & Shea, 1989

ETYMOLOGY. From Greek *parasitos* = parasite (*para* = beside, *sitos* = food), *tylos* = knob, *enchos* = spear (for 'parasitic *Tylenchus*').

The type species was found in *Ips typographus* (L.), in which a few large primary females and 200–300 small parasitic adults were found. The nematodes destroy the fat body and the beetle becomes weak and its reproduction ceases. In England about 5% of *Drosophila* populations were found parasitized by *P. diplogenus*. The nematodes destroyed the host's gonads and intestinal tract, particularly when emerging from the host; the normal exit was through the vulva (Welch, 1959). Iperti & Van Waerebeke (1968) report that in southern France, aphidiophagous ladybird (*Hormonia* spp.) populations were considerably reduced by parasitism with *P. coccinellinae*. *Parasitylenchus nearcticus* parasitizes *Drosophila recens* in New York State, USA. It sterilizes insect females and thus can be used as a biocontrol agent (Poinar *et al.*, 1997). *Parasitylenchus diplogenus* and *P. nearcticus*, which parasitize *Drosophila*, have the excretory pore located behind the nerve ring, unlike other species, which have it far forward.

## Subfamily Kurochkinitylenchinae Slobodyanyuk, 1999

### Diagnosis

Parasitylenchidae. Five distinct adult forms, **with two types of alternating heterosexual generation**. Three types of adult in host's body cavity – primary heterosexual female, secondary heterosexual female, and male of secondary heterosexual generation. Parasitic females sausage-shaped, dorsally curved when relaxed. Primary heterosexual female sausage- or spindle-shaped, produces heterosexual forms which multiply in the host's body cavity. **Copulation takes place in host's body cavity**. The secondary heterosexual female produces male and female juveniles that leave host for further development and copulation in the environment. Parasitic and partially free-living males slender, mobile, with short and thin stylet. Excretory pore generally anterior to nerve ring. Spermatozoa large-sized (diameter up to 7  $\mu\text{m}$ ). Spicules small, tylenchoid. Gubernaculum and a low bursa present. **Parasites of Siphonaptera**.

## Type genus

*Kurochkinitylenchus* Slobodyanyuk, 1999

No other genus.

**Genus *Kurochkinitylenchus* Slobodyanyuk, 1999**

(Fig. 163)

## Diagnosis

*Kurochkinitylenchinae*. **With three types of adult in host** – primary heterosexual female, secondary heterosexual female, and male. **Entomoparasitic forms: Primary heterosexual female:** Develops from preadult fertilized female that invades host's larva or pupa, and attains full maturity in adult host. **Sausage-shaped curving dorsally**, with wrinkled transverse folds and rounded ends, 0.37–0.65 mm long. Stylet strong, with basal thickenings, but not knobbed, 14–17  $\mu\text{m}$  long. Excretory pore anterior to nerve ring, excretory duct sclerotized. Vulva subterminal, lips not protruding. Vagina short, thin-walled. Uterus and oviduct forming two flexures with ovary tip facing forward. Spermatheca round to oval; in young females filled with spermatozoa 4–6  $\mu\text{m}$  in diameter. Uterus sac-like, extending to midbody, containing few eggs and juveniles. Ovoviviparous. Eggs about  $36\text{--}53 \times 20\text{--}28 \mu\text{m}$ . **Juveniles develop into bisexual forms in host's body cavity. Secondary heterosexual female:** About 0.38–0.72 mm long, dorsally curved, colourless, may be packed with eggs and juveniles. Cephalic cone absent. Stylet thin with minute basal swellings, 8–10  $\mu\text{m}$  long. **Excretory pore apical or at level of stylet; duct not as sclerotized as in primary heterosexual female.** Vulva a transverse, 11–15  $\mu\text{m}$  long slit. Vagina short, not sclerotized. Ovary and oviduct forming several flexures in anterior third of body. Tail conoid with rounded tip. Ovoviviparous. **Male of secondary heterosexual generation: In host's body cavity.** Mobile, 0.25–0.45 mm long, smaller than secondary female but not obese; as numerous as secondary females. Cephalic region continuous. Stylet reduced, with minute basal thickenings, 8–10  $\mu\text{m}$  long. Oesophagus reduced, glands not visible. Excretory pore between stylet and nerve ring. Testis outstretched; spermatozoa large-sized (three sperm occupying gonad width). Tail conoid-rounded to subcylindroid. Bursa low, extending to tail tip. Spicules cephalated, arcuate, small (14–17  $\mu\text{m}$ ). Gubernaculum present. **Copulation in host's haemocoel. Partially free-living forms:** Female 0.32–0.75 mm, male 0.32–0.59 mm long. Stylet 14–18 and 9–10  $\mu\text{m}$  long in female and male, respectively, with basal thickenings. Excretory duct sclerotized, opening anterior to nerve ring. Vulva lips not protruding. Ovary undeveloped, with six to ten oocytes. Vagina not formed completely. Tail elongate-conoid, with rounded tip. Spicules and gubernaculum well developed. Bursa low, enveloping tail. **Parasites of Siphonaptera.**

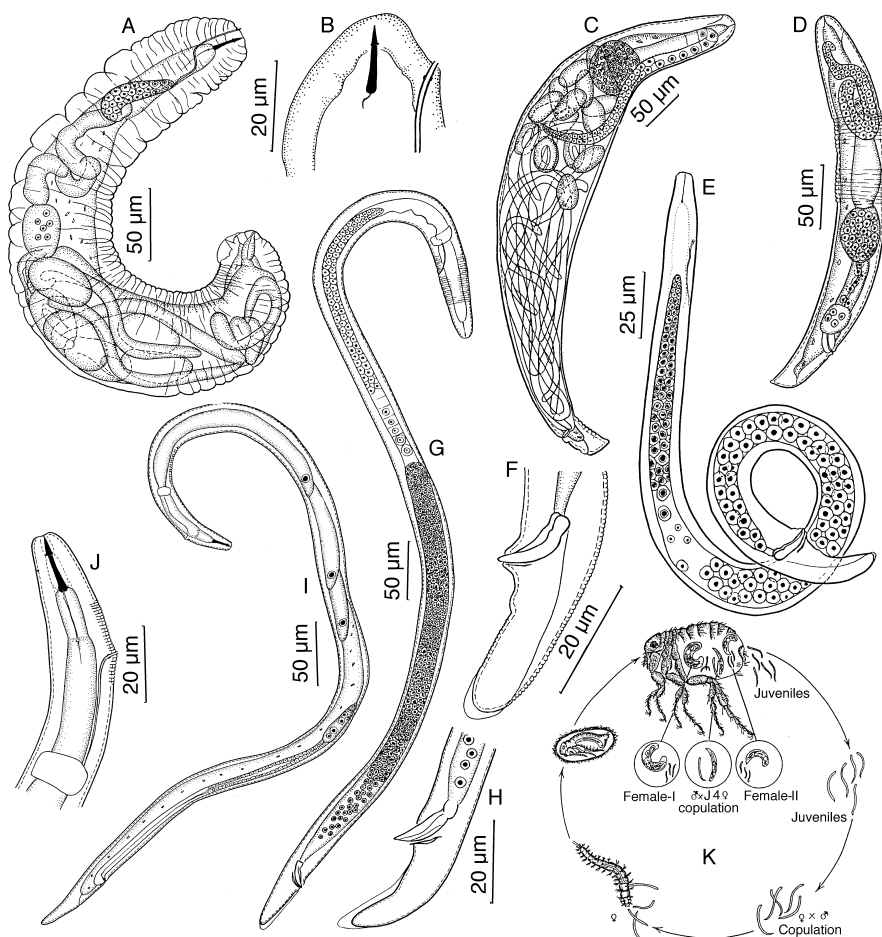
## Hosts

Siphonaptera: *Nosopsyllus*.

## Type species

*Kurochkinitylenchus laevicepsi* Slobodyanyuk, 1999

No other species.



**Fig. 163.** *Kurochkintylenchus laevicepsi* Slobodyanyuk. A. Mature primary heterosexual female. B. Head end of mature primary heterosexual female. C and D. Mature and young females of secondary parasitic heterosexual generation, respectively. E. Male of secondary parasitic generation. F. Tail end of male of secondary parasitic generation. G. Male of free-living generation. H. Tail end of male of free-living generation. I. Female of free-living generation. J. Anterior end of female of free-living generation. K. Life cycle. (After Slobodyanyuk (1999), courtesy *Russian Journal of Nematology*.)

**ETYMOLOGY.** Named in honour of the late Professor Y.V. Kurochkin, who first found and described some morphological forms of these nematodes, and *Tylenchus*.

The type species was collected from fleas, *Nosopsyllus laeviceps*, in the Kharabali district of the Astrakhan region, Russia.

## Subfamily Heterotylenchinae Siddiqi, 1986

### Diagnosis

Parasitylenchidae. Four distinct adult forms, **with alternation of heterosexual and parthenogenetic generations**. Two types of adult in host's body cavity, a primary heterosexual female and a secondary parthenogenetic female. **Parasitic females not dorsally curved. Adult male not found in host's body cavity**. Primary heterosexual female produces only female juveniles that develop to parthenogenetic females which, in turn, produce male and female juveniles that quit the host for further development and copulation. **Parasites of Diptera and Coleoptera**.

### Type genus

*Heterotylenchus* Bovien, 1937

### Other genera

*Paregletylenchus* Slobodyanyuk, 1984

*Wachekitylenchus* Slobodyanyuk, 1986

### Key to genera of Heterotylenchinae

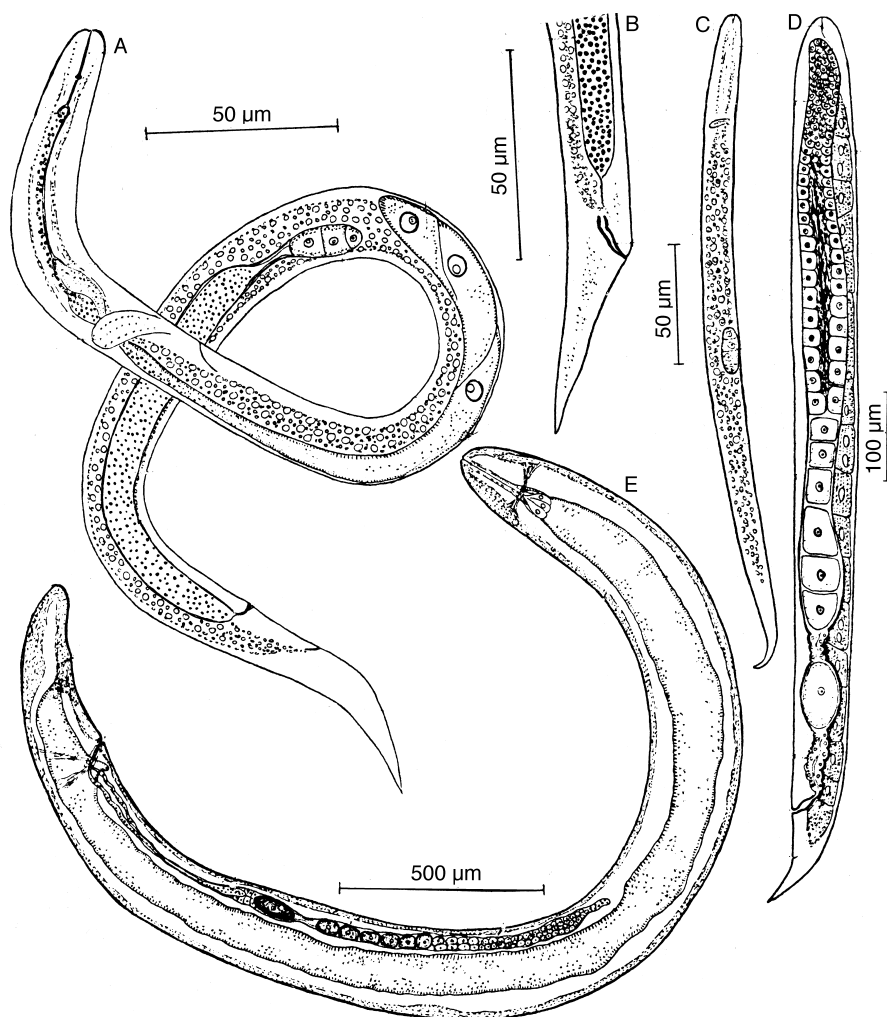
1. Cephalic lip areas and papillae in parasitic females prominent; male with six paired caudal 'papillae' ..... *Paregletylenchus*  
 Cephalic lip areas and papillae in parasitic females not prominent; male without caudal papillae ..... 2
2. Stylet with basal knobs present in entomoparasitic forms and juveniles; gubernaculum absent ..... *Heterotylenchus*  
 Stylet degenerate, without basal knobs in entomoparasitic forms and juveniles; gubernaculum present ..... *Wachekitylenchus*

### Genus *Heterotylenchus* Bovien, 1937

(Fig. 164)

### Diagnosis

Heterotylenchinae. **Entomoparasitic forms: Primary heterosexual female:** Parasitic in insect haemocoel and develops from female fertilized in the environment. Body obese, oval or elongate-cylindrical, straight to arcuate, about 3 mm long in type species. **Stylet knobbed**, may be sunken into body. Vulva near anus. Ovary small, not reflexed in type species, but may be reflexed once to several times. Oviparous with one to a few eggs in uterus at one time, as in type species, or ovoviparous with numerous juveniles in uterus. Eggs 100–150  $\mu\text{m}$  long in type species, being longer than those produced by parthenogenetic female. Eggs and juveniles develop to parthenogenetic females. **Secondary parthenogenetic female:** Vermiform, almost straight when relaxed, about 1 mm long and 75  $\mu\text{m}$  wide in type species. Stylet small (9–10  $\mu\text{m}$  long in type species), **knobbed**. Oesophagus degenerate. Rectum and anus vestigial. Tail conoid-pointed or obtuse with a spike. Ovary enormous, reaching into stylet region, oocytes arranged around a rachis in type species. Generally oviparous. **Juveniles:** Newly hatched 0.31–0.33 mm long,



**Fig. 164.** *Heterotylenchus aberrans* Bovien. A. Preadult infective female. B. Tail end of male. C. Second-stage juvenile. D. Mature parthenogenetic female from host. E. Mature gamogenetic female from host. (Redrawn after Bovien, 1937.)

17–18  $\mu\text{m}$  wide, with slender, 8–10  $\mu\text{m}$  long stylet lacking knobs in type species. Later-stage juveniles 0.4–0.45 mm long, **with knobbed stylet**, are ensheathed in previous stage cuticle. They invade host's ovary and aggregate in the oviduct to be laid in mock oviposition; those in the male insect cannot escape or develop further. Final moult and copulation in the environment. **Free-living forms: Female:** Partially free-living. About 0.5 mm long in type species. Cephalic region continuous, or slightly offset. **Stylet well developed, with distinct knobs**, 17  $\mu\text{m}$  long in type species. Orifice of dorsal gland at half or more stylet length behind stylet base.

**Excretory pore behind nerve ring; duct not strongly sclerotized.** Oesophagus cylindroid, non-muscular; gland elongated, extending over intestine to near mid-body. Vulva near anus. Uterus very long, packed with minute sperm when impregnated. Ovary immature, with few oocytes. **Male:** Slender, about as long as female. Stylet knobbed, shorter than in female (10  $\mu\text{m}$  long in type species). Tail conoid-rounded, about three anal body widths or less long. **Bursa absent.** Spicules prominently cephalated, arcuate, pointed, under 25  $\mu\text{m}$  long (18–20  $\mu\text{m}$  long in type species). **Gubernaculum absent**, or feebly developed.

#### Hosts

Diptera: *Delia*, *Morellia*, *Musca*.  
Coleoptera: *Bembidion*.

#### Type species

*Heterotylenchus aberrans* Bovien, 1937

#### Other species

*Heterotylenchus hyderabadensis* Reddy & Rao, 1980  
*H. simplex* Slobodyanyuk, 1975

ETYMOLOGY. Compound name from Greek *heteros* = other, and *Tylenchus*; the genus was probably named due to the newly discovered heterogonic mode of reproduction of its type species.

The type species was found by Bovien in 1932 parasitizing the body cavity of the onion fly, *Delia* (= *Hylemya*) *antiqua* (Meigen), in Denmark. The fly is a serious pest of onion. It hibernates in the pupa stage in the soil, but puparia are frequently found in onion bulbs. The rate of infection varied from 9 to 25%, and was equally high in both sexes. The female fly was generally sterilized by the nematode, as the male and female juveniles of the parthenogenetic females invaded the ovary and aggregated in the oviduct, waiting to escape via the genital aperture. The abundance of material helped Bovien (1937) to demonstrate for the first time the occurrence of heterogony in nematode reproduction.

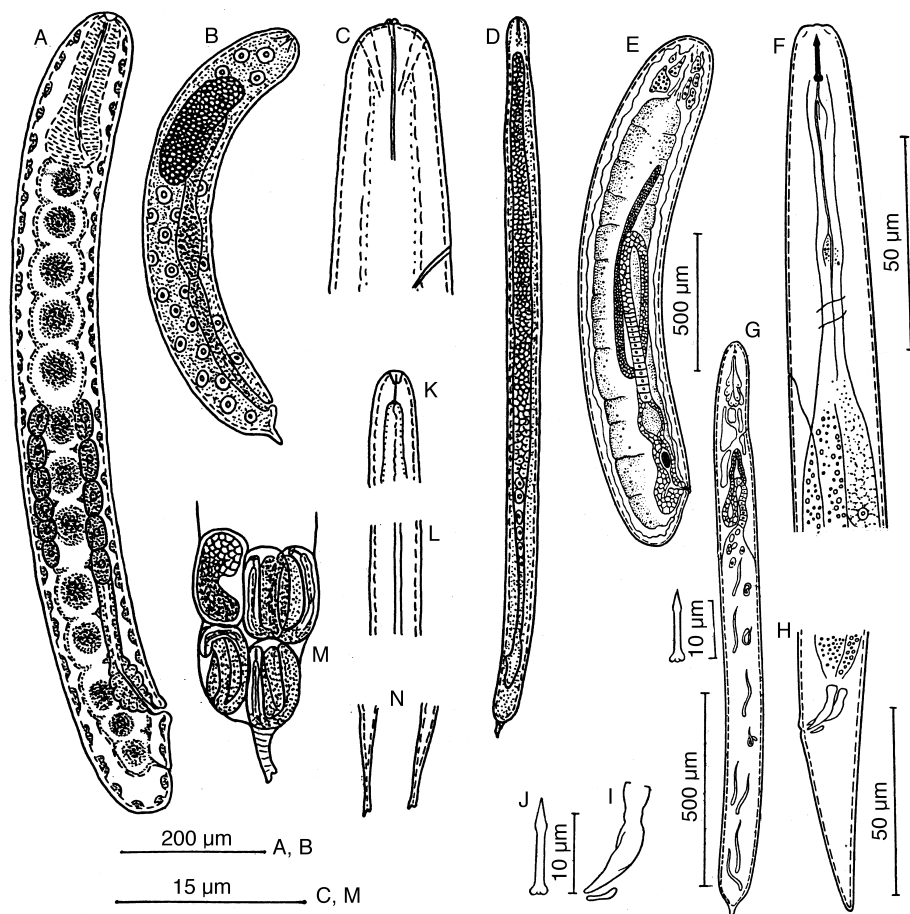
#### Genus *Wachekitylenchus* Slobodyanyuk, 1986

(Fig. 165)

#### Diagnosis

Heterotylenchinae. **Entomoparasitic forms: Primary heterosexual gamogenetic female:** Parasitic in Coleoptera haemocoel and develops from female fertilized in the environment. Body obese, usually bean-shaped, sometimes sausage-shaped, with ventral curvature, about 1–2 mm long. Cuticle lacking; hypodermis forms microvilli layer covering its surface for food absorption. **Stylet degenerate.** Vulva near anus, at 88–92% of body length. Ovary small, reflexed one to three times. Oviparous with one to a few eggs in uterus at one time, arranged in a row. Eggs and juveniles develop to parthenogenetic females. **Secondary parthenogenetic female:** Vermiform, ventrally arcuate or straight when relaxed, about 2.0–2.5 mm long





**Fig. 165.** *Wachekitylenchus bovienii* (Wachek) Slobodyanyuk. A and E. Adult gamogenetic females. B. Young gamogenetic female. C. Head end of parthenogenetic female. D and G. Young and mature parthenogenetic females, respectively. F. Anterior end of male. H. Tail end of male. I. Spiculum and gubernaculum. J. Stylet of male. K. Head end of second-stage gamogenetic juvenile. L and N. Midbody region and tail ends, respectively, of second-stage gamogenetic juveniles. M. Tail end of old parthenogenetic female. (A–D and K–N. After Chizhov & Zakharenkova (1993). E–J. After Wachek (1955).)

( $a = 15.8\text{--}20.6$ ). Stylet, oesophagus and vulva degenerate. Rectum and anus vestigial. Tail conoid-pointed or obtuse with a spike. Ovary enormous, reaching nearly to anterior end. Numerous eggs produced and are deposited in body cavity; viviparous. Degenerate males seen in anterior part of body. **Juveniles:** Newly hatched juveniles  $0.32\text{--}0.35$  mm long, with slender stylet  $8\text{--}10\text{ }\mu\text{m}$  long, knobs indistinct. Tail elongate conoid. Free-living males and females have distinct intestinal lumen. **Gubernaculum present.**

## Hosts

Coleoptera: *Bembidion*, *Clivia*.

## Type species

*Wachekitylenchus bovienii* (Wachek, 1955) Slobodyanyuk, 1986  
syn. *Heterotylenchus bovienii* Wachek, 1955

## Other species

*Wachekitylenchus bembidi* Zakharenkova & Chizhov, 1991  
*W. stammeri* (Wachek, 1955) Slobodyanyuk, 1986  
syn. *Heterotylenchus stammeri* Wachek, 1955  
*W. wuelkeri* (Wachek, 1955) Slobodyanyuk, 1986  
syn. *Heterotylenchus wuelkeri* Wachek, 1955

## Relationship

*Wachekitylenchus* is differentiated from *Heterotylenchus*, *Paregletylenchus* and *Psyllotylenchus* in the bean-shaped body of the heterosexual female, in the presence of cephalic labia, the stylet structure, viviparity, presence of a gubernaculum and of an intestinal lumen in free-living males and females.

ETYMOLOGY. Patronym honouring F. Wachek.

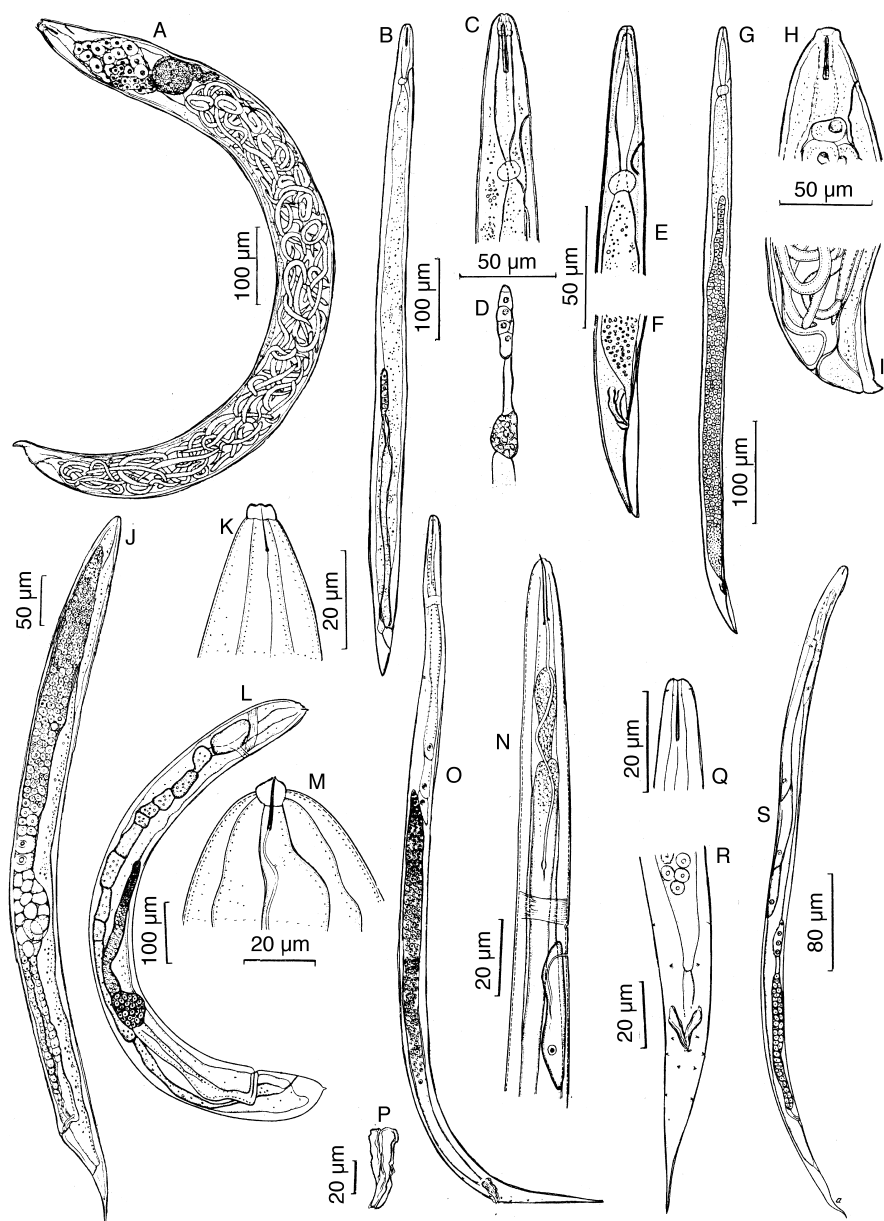
The type species was found by Wachek (1955) in Germany parasitizing *Bembidion varium* Oliv. and *B. obliquum* Strm. (Coleoptera: Carabidae).

## Genus *Paregletylenchus* Slobodyanyuk, 1984

(Fig. 166, J–S)

## Diagnosis

Heterotylenchinae. **Entomoparasitic forms: Primary heterosexual female:** Body obese, elongate-cylindrical, 1–2 mm long, ventrally arcuate;  $a = 9.5$ –18.8. Cephalic region rounded or with small cone. Tail end rounded, with spike-like projection at tip. Intestine without lumen. **Stylet well developed with thickened base but without knobs**, 15–17  $\mu\text{m}$  long. Genital tube about half as long as body. Oviparous. **Secondary parthenogenetic female:** Body almost straight and spindle-shaped, 0.52–0.96 mm long. Cephalic region narrower than body, **with six distinct lip areas** bearing prominent papillae. Stylet weak, slightly widened at base, 8.5–12.5  $\mu\text{m}$  long, genital tube filling most of body cavity. Preuterine gland (= spermatheca) large, spheroidal. Oviparous. **Partially free-living forms: Female:** Body slender, straight to ventrally arcuate, 0.51–0.64 mm long. Cephalic region offset, with large papillae. Stylet well developed; base thickened but without knobs. Oesophagus cylindrical, with wide lumen, three long glands; orifice of dorsal gland at one stylet length behind stylet base; those of subventral glands near middle of oesophagus. Uterus elongate, with sperm. **Male:** Stylet rod-like, less developed than in female. Oesophageal glands shorter than those in female. Testis well developed; sperm relatively large. No bursa or gubernaculum. Spicules 14.3–17.5  $\mu\text{m}$  long. **Tail with paired ‘caudal papillae’**, three pairs preanal and as many postanal.



**Fig. 166.** A–I. *Spilotylenchus arthuri* Launay, Deunff & Bain. J–S. *Paregletylenchus papillatus* Slobodyanyuk. A, H, I, L and M. Entomoparasitic adult gamogenetic females. B–D, N and S. Entomoparasitic preadult gamogenetic females. J and K. Entomoparasitic parthenogenetic female. E–G and O–R. Free-living males. A, B, J, L and S. Entire females. G and O. Entire males. C, E, H, K, M and Q. Anterior ends. F, I and R. Posterior ends. D. Ovary and spermatheca. P. Spicules. (A–I. Redrawn after Launay *et al.* (1983). J–S. Redrawn after Slobodyanyuk (1984).)

## Host

Diptera: *Paregle* (Anthomyiidae).

## Type species

*Paregletylenchus papillatus* Slobodyanyuk, 1984

No other species.

## Note

*Paregletylenchus* is very similar to *Heterotylenchus*, differing from it in the presence of well-marked lip areas and papillae and caudal papillae in the male. The occurrence of three pairs of preanal and as many postanal papillae is quite unusual for Tylenchida and needs confirmation.

ETYMOLOGY. From the generic name of its type host, *Paregle cinerella* Flln., and *Tylenchus*.

## Subfamily Spilotylenchinae Slobodyanyuk, 1999 syn. Psyllotylenchinae Slobodyanyuk, 1999

## Diagnosis

Parasitylenchidae. Parasitic females with dorsally curved bodies (except *Incurvinema*). One or two types of adult in host's body cavity, with or without alternation of heterosexual and parthenogenetic generations. **Adult male not found in host's body cavity. Female stylet generally with basal thickenings, not knobbed. Vulva not deeply cleft.** Male and female juveniles quit the host for further development and copulation. **Parasites of Siphonaptera.**

## Type genus

*Spilotylenchus* Launay, Deunff & Bain, 1983

## Other genera

*Incurvinema* Deunff, Launay & Beaucournu, 1985

*Psyllotylenchus* Poinar & Nelson, 1973

## Key to genera of Spilotylenchinae

1. Only one type of female parasitic in insect haemocoel known; excretory pore in heterosexual female behind stylet base; excretory duct in free-living forms cuticularized ..... *Spilotylenchus*  
Two types of female in insect haemocoel; excretory pore in heterosexual female opposite or near stylet base; excretory duct in free-living forms not cuticularized ..... 2
2. Heterosexual female ventrally curved; preuterine gland in parthenogenetic female elongate; male spirally curved ..... *Incurvinema*  
Heterosexual female dorsally curved; preuterine gland in parthenogenetic female spherical; male not spirally curved ..... *Psyllotylenchus*

## Genus *Spilotylenchus* Launay, Deunff & Bain, 1983

(Fig. 166, A–I)

### Diagnosis

*Spilotylenchinae*. **Entomoparasitic female:** Elongate-obese, dorsally curved, 0.9–1.3 mm long, maximum width 75–116  $\mu\text{m}$  in type species; cephalic and tail region not deformed. Stylet robust, in normal position, 24–26  $\mu\text{m}$  long in type species, **without basal knobs or thickenings**. **Excretory pore well anterior to nerve ring**. Uterus of old females enormous, occupying about half or more of body cavity, packed with eggs and juveniles. Ovary coiled in anterior region. Tail end conoid, dorsally curved. Vulva prominent, close to anus, which is often distinct. Ovoviviparous. Parthenogenetic female not found. **Partially free-living forms:** **Female:** Body straight, 0.54–0.75 mm long, maximum width 24–33  $\mu\text{m}$ . **Excretory pore between stylet base and nerve ring, duct cuticularized. Stylet robust, without basal knobs or thickenings**. Vulva transverse, with slightly raised lips near anus. Ovary rudimentary, with three to six oocytes in type species. Tail about twice anal body width long, conoid with rounded or pointed tip. **Male:** About as long as female. Excretory pore anterior to nerve ring but behind stylet base. Testis outstretched. Spicules cephalated, arcuate, 14–18  $\mu\text{m}$  long in type species. Gubernaculum present. Bursa prominent, completely enveloping tail.

### Hosts

Siphonaptera: *Ceratophyllus*, *Coptopsylla*, *Nosopsyllus*, *Spilopsyllus*.

### Type species

*Spilotylenchus arthuri* Launay, Deunff & Bain, 1983

### Other species

*Spilotylenchus beaucournui* Launay & Deunff, 1984

*S. ivashkini* Slobodyanyuk, 2000

*S. laplandicus* (Rubzov & Darskaja in Rubzov, 1981) Launay, Deunff & Bain, 1983  
syn. *Neoparasitylenchus laplandicus* Rubzov & Darskaja in Rubzov, 1981

*S. maisonabei* Launay & Deunff, 1990

*S. megabothridis* (Laumond & Beaucournu, 1978) Launay, Deunff & Bain, 1983  
syn. *Neoparasitylenchus megabothridis* Laumond & Beaucournu, 1978

*S. pawlowskyi* (Kurochkin, 1960) Slobodyanyuk, 1997  
syn. *Heterotylenchus pawlowskyi* Kurochkin, 1960

*Psyllotylenchus pawlowskyi* (Kurochkin) Poinar & Nelson, 1973

*S. ussuriensis* Litvinova, 1995

ETYMOLOGY. From prefix of host's name *Spilopsyllus*, and *Tylenchus*.

The type species parasitizes the European rabbit flea, *Spilopsyllus cuniculi* (Dale), in France. Parasitism has a blocking effect on the flea oogenesis but spermatogenesis in the male flea is unaffected. *Spilotylenchus pawlowskyi* was originally described as *Psyllotylenchus pawlowskyi* from two flea species, *Coptopsylla lamellifer* and *Nosopsyllus laeviceps*. Slobodyanyuk (1997) collected specimens from fleas in the type locality,

designated a neotype (from the flea *C. lamellifer*) because the type material was destroyed or lost, and transferred the species to the genus *Spilotylenchus*. A key to *Spilotylenchus* spp. based on gravid females is given by Launay & Deunff (1990).

### Genus *Psyllotylenchus* Poinar & Nelson, 1973

syn. *Aphanitylenchus* Rubzov, 1981

(Fig. 152, K–O)

#### Diagnosis

Spilotylenchinae. Alternation of heterosexual cycle with a parasitic parthenogenetic cycle in host's body cavity. **Both heterosexual and parthenogenetic females ovo-viviparous and dorsally curved** with ventral side turned outward. **Entomoparasitic forms: Primary and heterosexual female: Sausage-shaped**, 0.8–1.5 mm long in type species, white. Cephalic and tail regions not overgrown by body expansion. Stylet present in normal position, 15–20 µm long. **Excretory pore near stylet base**. Anus distinct. Tail conical, with a mucro in type species. **Secondary parthenogenetic female:** Obese, 0.36–0.84 mm long, with indistinct stylet, large quadricolumella, a large spherical preuterine gland and rounded tail in type species. **Partially free-living forms:** In the burrow or nest of the flea's host. Elongate-slender worms with round continuous symmetrical cephalic region and conical tail. **Female:** About 0.5–0.7 mm long, in type species stylet 17–18 µm long, with basal thickenings; excretory pore anterior to nerve ring and oesophageal glands extending beyond the middle of the body. Vulva close to anus. Ovary immature. **Male:** About the size of the female, with indistinct stylet. Testis outstretched or reflexed. Spicules small (11–13 µm long in type species). Gubernaculum present. Bursa enveloping tail in type species, but may be absent. Male dies after mating, body not spirally curved. Impregnated female invades flea larva and matures in the host's haemocoel.

#### Hosts

Siphonaptera (fleas): *Catallagia*, *Ceratophyllus*, *Coptopsylla*, *Diamanus*, *Monopsyllus*, *Neopsylla*, *Spilopsyllus*.

#### Type species

*Psyllotylenchus viviparus* Poinar & Nelson, 1973

#### Other species

*Psyllotylenchus acuticapitus* Rubzov & Tshumakova, 1981

*P. caspius* Rubzov & Samurov in Rubzov, 1981 (syn. of *P. pawlowskyi* for Slobodyanyuk, 1997)

*P. chabaudi* Deunff & Launay, 1984

*P. crassus* (Rubzov & Tshumakova, in Rubzov, 1981) Siddiqi, 1986

syn. *Aphanitylenchus crassus* Rubzov & Tshumakova, in Rubzov, 1981

*P. curvans* Rubzov & Kotty, in Rubzov, 1981

*P. cuspidatus* (Rubzov & Tshumakova, in Rubzov, 1981) Siddiqi, 1986

syn. *Aphanitylenchus cuspidatus* Rubzov & Tshumakova, in Rubzov, 1981

*P. ioffi* Rubzov & Morozov, in Rubzov, 1981 (syn. of *P. pawlowskyi* for Slobodyanyuk, 1997)

- P. kozlovi* Rubzov & Tshumakova, in Rubzov, 1981  
*P. larviparus* Rubzov & Tshumakova, in Rubzov, 1981  
*P. latifrons* Rubzov & Tshumakova, in Rubzov, 1981  
*P. longicauda* (Rubzov & Tshumakova, in Rubzov, 1981) Siddiqi, 1986  
     syn. *Aphanitylenchus longicauda* Rubzov & Tshumakova, in Rubzov, 1981  
*P. macrocephalus* Rubzov & Morozov, in Rubzov, 1981 (syn. of *P. pawlowskyi* for  
     Slobodyanyuk, 1997)  
*P. morozovi* Rubzov, 1981 (syn. of *P. pawlowskyi* for Slobodyanyuk, 1997)  
*P. neopsyllus* Rubzov & Tshumakova, in Rubzov, 1981  
*P. rectangulatus* Rubzov, 1982  
*P. samurovi* Rubzov, 1981  
*P. tenuis* Rubzov & Tshumakova, in Rubzov, 1981  
*P. tilflovi* Rubzov & Tshumakova, in Rubzov, 1981  
*P. zassuchini* Rubzov & Morozov, in Rubzov, 1981 (syn. of *P. pawlowskyi* for  
     Slobodyanyuk, 1997)

### Nomen nudum

*Neonema ctenophthalmi* Pavlosky, 1927 (a nematode from fleas)

ETYMOLOGY. From Greek *psyllos* = flea (the host), *tylos* = knob, and *enchos* = spear.

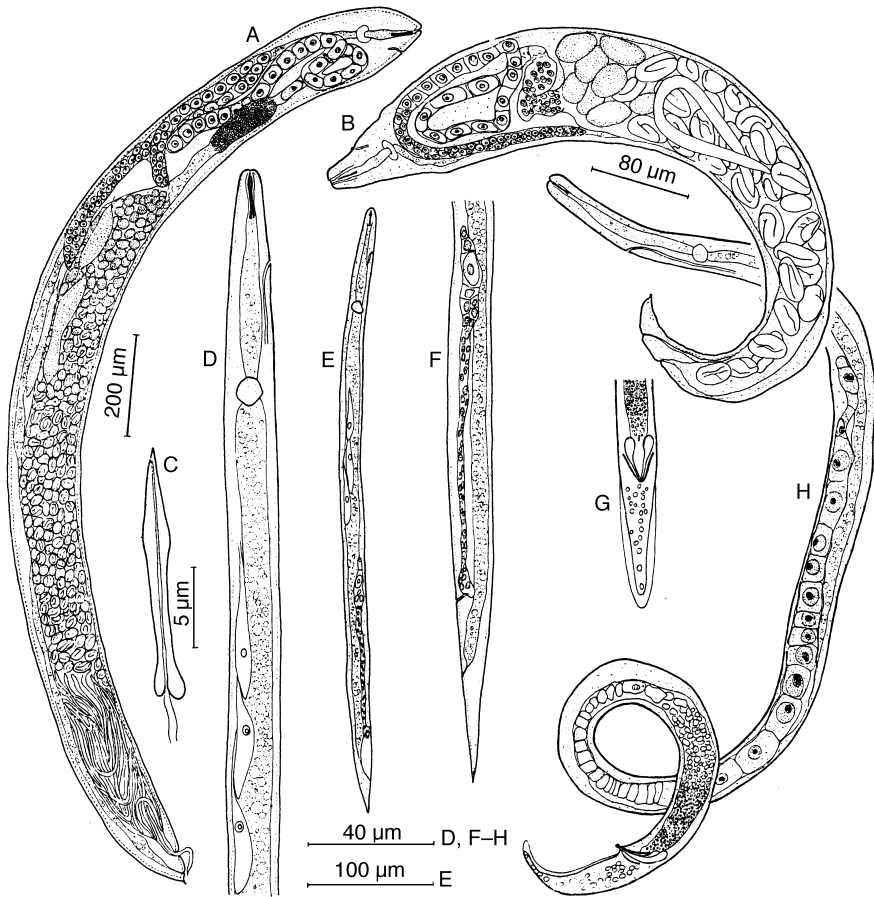
The type species was found parasitizing a flea, *Monopsyllus ciliatus protinus* (Jordan) collected from the chipmunk (*Eutamias townsendi senex* (Allen)) in California, USA. Parasitized fleas are generally castrated. Nematodes copulate in the environment, and the impregnated female penetrates the host through the cuticle. Juveniles produced by this female remain in the flea's haemocoel and develop into parthenogenetic females, which in turn produce juveniles, which leave the host as third or fourth stage via the rectum or oviduct of the host (Poinar & Nelson, 1973).

### Genus *Incurvinema* Deunff, Launay & Beaucournu, 1985

(Fig. 167)

#### Diagnosis

Spilotylenchinae. **Entomoparasitic forms: Primary heterosexual female:** Body obese, elongate-cylindrical, 1.1–2.1 mm long, **ventrally arcuate**; maximum width 125–185 µm. Cephalic region rounded or with small cone. Excretory pore opposite stylet base. Tail conical, with pointed terminus. **Stylet well developed with thickened base but without knobs**, 16 µm long. Spermatheca elongate cylindrical. Uterus extends to two-thirds body length, contains many eggs and juveniles. **Ovoviviparous. Secondary parthenogenetic female:** Body fusiform, dorsally curved, 0.57–0.83 mm long. Ovoviviparous. Cephalic region rounded-truncate. stylet weak, reduced, 8.8–12.0 µm long. Genital tube filling most of body cavity. Preuterine gland elongate. Vulva about one tail length from anus. Uterus about two-thirds body length long, filled with eggs and juveniles. Ovary coiled between oesophagus and uterus. **Tail conoid-pointed. Partially free-living forms: Female:** Body slender, straight to ventrally arcuate, 0.4–0.47 mm long. Excretory pore well anterior to nerve ring, about one body width behind stylet. Stylet well developed; base



**Fig. 167.** *Incurvinema helicoides* Deunff, Launay & Beaucournu. A. Gamogenetic female. B. Parthenogenetic female. C. Stylet of gamogenetic female. D and F. Anterior and posterior region, respectively, of partially free-living female. E. Partially free-living female. G. Tail end of male. H. Male. (After Deunff *et al.*, 1985.)

thickened but without knobs. Three long glands extending over intestine dorsally. Uterus elongate, with relatively few sperm. **Male:** Body spirally curved on death. Stylet rod-like, less developed than in female. Testis well developed with large spermatocytes arranged serially; sperm relatively large. Bursa low, enveloping tail. Spicules strong, 14–18 µm long. Gubernaculum present, 7–14 µm long. Tail ventrally arcuate.

#### Host

Siphonaptera: *Rhadinopsylla* (Hystrichopsyllidae).



## Type species

*Incurvinema helicoides* Deunff, Launay & Beaucournu, 1985

No other species.

## Note

*Incurvinema* is difficult to differentiate from *Psyllotylenchus* and *Spilotylenchus*. In *Psyllotylenchus* both heterosexual and parthenogenetic females are ovoviviparous, body curvature is dorsal and the parthenogenetic female has a large rounded preuterine gland and a hemispherical to subclavate tail. *Aphanitylenchus* has a dorsally curving heterosexual female and lacks a stylet in the parthenogenetic female. Its generic diagnosis is imprecise (Deunff *et al.*, 1985) and it was considered as a synonym of *Psyllotylenchus* by Siddiqi (1986).

ETYMOLOGY. From 'incurving' (ventral curving) heterosexual female, and *nema* = nematode.

The type species is a parasite of *Rhadinopsylla pentacantha* (Siphonaptera, Hystrichopsyllidae), common on moles, *Talpa europae* (Arvicolidae), in France.

## Subfamily Heteromorphotylenchinae Siddiqi, 1986

## Diagnosis

Parasitylenchidae. Four distinct adult forms, with alternation of heterosexual and parthenogenetic generations. **Parthenogenetic generation in free life outside host.** Parasitic heterosexual female in host produces female juveniles, which have full development in host and leave host through anus just before the last moult. Last-stage juveniles moult in the environment to become **non-feeding parthenogenetic females**, which survive on their food reserve. Eggs produced by parthenogenetic females hatch and the juveniles develop into heterosexual males and preadult females, which mate. Preadult fertilized females invade host's larvae, pupae or nymphs.

## Type genus

*Heteromorphotylenchus* Remillet & van Waerebeke, 1978

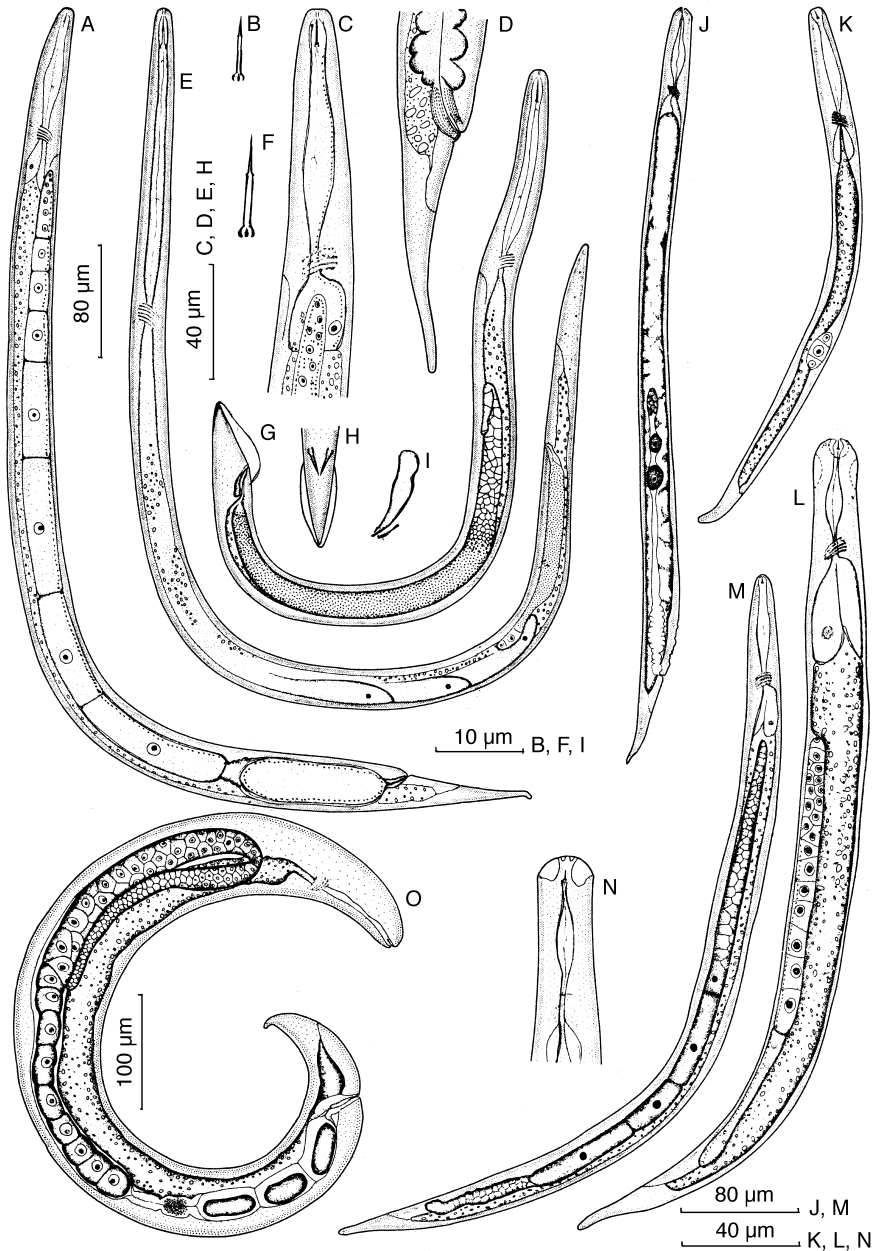
No other genus.

## Genus *Heteromorphotylenchus* Remillet & van Waerebeke, 1978

(Fig. 168)

## Diagnosis

Heteromorphotylenchinae. **Entomoparasitic forms: Heterosexual female:** In insect haemocoel. Partially obese but **vermiform** ( $a = 10\text{--}18$ ), about 1 mm long, dorsally curved in arcuate to spiral shape, colourless. Cephalic end rounded. Stylet about 10  $\mu\text{m}$  long, knobbed, in normal position. Oesophageal glands degenerate. Vulva distinct, at 84–94% of body length. Ovary reflexed once; oocytes in several rows. Uterus rarely with more than three eggs. Eggs about 50  $\mu\text{m} \times 22 \mu\text{m}$ , continuously laid in host. Rectum and anus present. Tail short, conoid, with ventral side



**Fig. 168.** *Heteromorphotylenchus stolidotae* Remillet & van Waerebeke. A–D. Partially free-living parthenogenetic female. E and F. Preadult infective female and its stylet. G–I. Free-living male. J–N. Partially free-living parthenogenetic generation. O. Entomoparasitic gamogenetic female. A and J. Females. B. Stylet. C and N. Anterior ends. D and H. Tail ends. I. Spicule and gubernaculum. K. Second-stage juvenile. L, M and N. Third-stage juveniles. (Redrawn after Remillet & van Waerebeke, 1978.)

convex. Parthenogenetic female not found in host's body cavity. Second-stage juveniles about 0.2 mm long, have a stylet, short cylindroid tail and genital primordium three-celled a little behind middle of body. Juveniles in host, numbering several hundred, develop to preadult females only which emerge through host's anus almost every day. **Partially free-living forms: Parthenogenetic female: Non-feeding,** survives on food reserve. Smaller and more slender than parasitic female ( $L = 0.5\text{--}0.8$  mm,  $a = 17\text{--}23$  in type species). Cephalic region rounded, continuous. Stylet about  $10\text{ }\mu\text{m}$  or less long, with distinct basal knobs. Orifice of dorsal gland close to stylet base. Oesophagus fusiform; glands reduced, only dorsal gland seen. Excretory pore near nerve ring. Vulva at about 87–90% of body length. Postvulval uterine sac absent. Ovary outstretched, with one or two rows of oocytes. Uterus with only one egg at one time. Eggs produced in small numbers,  $76\text{--}84 \times 30\text{--}34\text{ }\mu\text{m}$  in type species. Eggs hatch and juveniles develop to heterosexual preadult females and adult males which copulate and impregnated females invade insect larva, pupa or nymph. **Heterosexual female:** Partially free-living. Small-sized ( $0.3\text{--}0.33$  mm long in type species), slender. Cephalic region continuous, rounded. Stylet knobbed,  $10\text{--}12\text{ }\mu\text{m}$  long in type species. Corpus elongate-cylindroid. Oesophageal glands enlarge, extending to middle of body or beyond; subventral glands longer than the dorsal gland. Vulva posterior, at 83–87% of body length in type species; lips indistinct. Ovary rudimentary. Uterus elongated, packed with minute sperm when fertilized. Tail short, conoid-rounded. Further development in insect haemocoel. **Male:** About as long as heterosexual free-living female, with shorter ( $6\text{--}8\text{ }\mu\text{m}$  long) stylet and reduced oesophageal glands. Testis outstretched; vas deferens packed with minute sperm. Spicules cephalated, ventrally arcuate,  $11\text{--}13\text{ }\mu\text{m}$  long in type species. Gubernaculum simple. Bursa completely enveloping tail.

## Hosts

Coleoptera: (Nitidulidae): *Carpophilus*, *Stelidota*.

## Type species

*Heteromorphotylenchus stelidotae* Remillet & van Waerebeke, 1978

## Other species

*Heteromorphotylenchus carpophili* Remillet & van Waerebeke, 1978

ETYMOLOGY. From Greek *heteros* = other, *morphé* = form, *tylos* = knob, and *enchos* = spear.

The type species parasitizes *Stelidota remilleti* Endrödy-Younga (Nitidulidae), found in decomposing fruits in soil in Tananarive region, Malagasy. *Heteromorphotylenchus carpophili* is parasitic in *Carpophilus fumatus* Boheman, *C. mutilatus* Erichson and *C. notatus* Murray. The parasitic female develops in a transparent membrane produced by tissue reaction of the host. Eggs are laid continuously and accumulate inside the membrane. The juveniles have the first moult within the egg, the second soon after hatching, and develop to fourth-stage female juveniles which are similar to adults and which leave the host via the rectum. The last moult occurs in the environment. The female lays eggs which may be enclosed in the shed cuticle as a string with

three to seven eggs. Total mean egg production by the female is seven, maximum 14. The eggs are laid and hatch in decaying fruits or in the corpses of dead insects. These juveniles develop to males and females. The fertilized female penetrates the host, attains maturity in the nymph and lays eggs after the nymph moults.

The most important point in the life cycle is the occurrence of a secondary parthenogenetic female in the environment, instead of in the host as in *Heterotylenchus*. This parthenogenetic female lives on its food reserve and does not feed. A small number of eggs are produced. The female survives several months after it has laid eggs. It is a continuum of the entomoparasitic phase and should not be confused with the free-living females of the Neotylenchoidea (cf. *Deladenus*, *Fergusobia*), which have a normal oesophagus and feed and keep on reproducing freely in the environment.

Infected nitidulid females are rendered sterile by the nematode; parasitized male insects are not sterilized. In Tananarive, Malagasy, a maximum of 800 juveniles was found in one *Stelidota*; up to 12% of the population was infected in November, but the parasitism of *Carpophilus* by *H. carpophili* was only 2–7% in Tananarive, Tulear and Morondava (Remillet & van Waerebeke, 1978).

## Genera Dubia in Hexatylinia

### Genus *Anguillonema* Fuchs, 1938

(Fig. 147, K–N)

#### Diagnosis

Hexatylinia. Only 'free-living' forms known. **Female:** Body 0.47–0.96 mm long, vermiform ( $a = 15\text{--}18$  in type species). Cephalic region low, flattened. Stylet small, knobbed. Excretory pore anterior to nerve ring but considerably behind stylet base. Oesophagus cylindroid, non-muscular. Ovary well developed, reaching oesophageal region, with oocytes in several rows, apparently arranged around a rachis. Spermatheca oval, with minute round sperm. Uterus elongate, with several developing eggs. Eggs  $34\text{--}41 \times 14\text{--}20 \mu\text{m}$  in type species. Vulva at 90–94%, lips protuberant. Vulva–anus distance shorter than tail length. **Tail conoid with tip dorsally bent, hook-like** in type species. **Male:** Stylet knobbed. Excretory pore midway from stylet base to nerve ring. **Spicules very long**, about as long as tail, cephalated. Gubernaculum present. **Bursa absent**. Tail conoid-pointed; posterior half hooked dorsally.

#### Type species

*Anguillonema poligraphi* Fuchs, 1938 (= sp. inq.)

#### Other species

*Anguillonema crenati* Fuchs, 1938 (= sp. inq.)

#### Remarks

The designated type species of *Anguillonema* is *A. poligraphi*, as stated by Fuchs (1938, p. 132), and not *Anguillonema pinguicauda* Fuchs, 1938 (now under *Prothallonema*), as given by Baker (1962) and Massey (1974). Fuchs (1938) stated that he found

specimens of *A. poligraphi* in 1930 and of *A. crenati* in 1932 and that at first he had listed them under the generic name *Tylenchonema* with *poligraphi* as the type species, but later he withdrew the name in favour of *Tylenchinema* Goodey, and instead, proposed the name *Anguillonema* for it when he (1938) described the two species. Thus, Fuchs' designation of *poligraphi* as type species of *Tylenchonema* should be considered as applying to *Anguillonema*, since the latter was intended to be a replacement name for the former.

The gravid females of the two species recovered from the beetle frass could have been either the free-living fungus-feeding forms, free-living non-feeding forms (cf. *Heteromorphotylenchus*), or insect-parasitic forms liberated by the accidental crushing of the beetles during the collection procedure (cf. secondary heterosexual/parthenogenetic females of *Parasitylenchus*, *Heterotylenchus*). It is not certain that the male described by Fuchs (1938) for *A. poligraphi* belongs to that species. *Anguillonema* is of uncertain status and should be considered as a genus dubium. *Anguillonema poligraphi* and *A. crenati* are considered here as species inquirendae.

ETYMOLOGY. From Latin *anguilla* = eel, and *nema* = nematode.

The type species was found in decaying frass in galleries of beetles (*Poligraphus poligraphus* L.) in Germany. *Anguillonema crenati* was recovered from frass of *Hylesinus crenatus* Fab. from Holland.

### Genus *Helionema* Brzeski, 1962

(Fig. 169, G–I)

#### Diagnosis

Hexatylinea. **Only pre-parasitic, unimpregnated female known.** Small-sized (0.43 mm), slender ( $a = 33$ ). Cuticle annulated except at lip region, which is 'chitinized' but not set off by a constriction, and bearing at its base four small, hardly visible, cephalic papillae. Stylet cylindroid, massive, about twice lip region width long, with distinct lumen, lacking basal knobs; guiding ring single, at anterior third of stylet. Orifice of dorsal gland at less than half stylet length behind stylet base. Oesophagus with oblong median bulb, nearly four times as long as body width at base of lips, without valve plates. **Basal bulb glandular.** Female gonad short, prodelphic, about six times vulval body width long, bent at two-thirds of its length. Vulva at 71.4%, over two body widths from anus. **Postvulval uterine sac present**, about as long as body width at vulva. Rectum and anus distinct. Tail elongate-conoid, about 60  $\mu\text{m}$  long, with a terminal spike-like mucro. Possibly parasitic in insect haemocoel in adult stage.

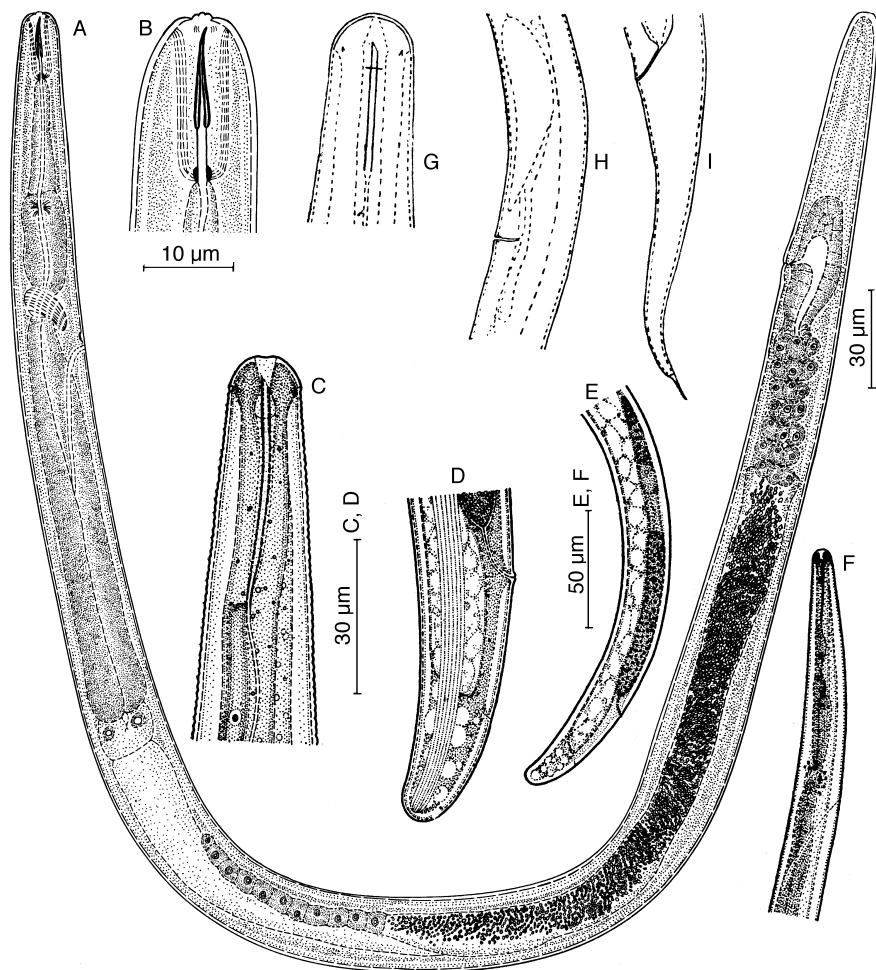
#### Type species

*Helionema gracile* Brzeski, 1962 (= sp. inq.)

No other species.

#### Remarks

Brzeski (1962) pointed out that the stylet of *Helionema gracile* is like that of the genus *Dorylaimus* and that the genus is close to *Dotylophus* Andr ssy, 1958 (Fig. 169,



**Fig. 169.** A and B. *Robleus cylindricus* Massey. C–F. *Dotylaphus* (= *Deladenus*) *ruehmi* Andrassy. G–I. *Helionema gracile* Brzeski. A. Female. B, C and G. Head ends of females. D, E and I. Posterior regions. F. Oesophageal region. H. Vulval region. (A and B. After C.L. Massey (1974). C–F. After I. Andrassy (1958). G–I. After Brzeski (1962).)

C–F) (now a synonym of *Deladenus*), especially in the stylet structure, but differs from it in the structure of the oesophagus. He also remarked that, in the absence of valve plates in the median bulb of the oesophagus, the family Helionematidae is similar to Nothotylenchinae, differing in the stylet structure and the considerably larger size of the bulb. Unfortunately, the oesophagus was not illustrated.

*Helionema gracile* has an oesophagus similar to that of the nematodes now placed in the family Sphaerulariidae. Type specimens of *H. gracile* were not available for study. On the basis of the available information, *Helionema* and *H. gracile* were proposed by Siddiqi (1986) as genus dubium and species inquirenda, respectively; Helionematidae was considered a family of uncertain status in Hexatylini.

ETYMOLOGY. Greek *helios* = sun, and *nema* = nematode.

The three females of the type species were found in lower layers of dead leaves in a small tuft of peat moss (*Sphagnum* sp.) in Białowieśka Forest, Poland.

### **Genus *Robleus* Massey, 1974**

(Fig. 169, A & B)

#### **Diagnosis**

Hexatylinea. **Only pre-parasitic impregnated female known.** Body elongate-cylindroid ( $L = 0.62\text{--}0.68$  mm;  $a = 28\text{--}32$ ). Cuticle finely striated; lateral incisures not discernible. Cephalic region broadly rounded, continuous; framework inconspicuous. Stylet  $19\text{ }\mu\text{m}$  long, reminiscent of that of *Paratylenchus*, with conus heavily sclerotized, bent ventrally at tip and measuring two-thirds of total stylet length; basal knobs small, rounded. Oesophagus cylindroid, non-muscular, nerve ring at end of its anterior two-fifths. A tri-nucleate cardia-like structure at base of oesophagus. Orifice of dorsal oesophageal gland not seen. Excretory pore just behind nerve ring. Vulva at 87%, lips slightly raised. Vagina very short. A short postvulval uterine sac present. Uterus with a quadricolumella, anterior to which several hundred minute round sperm fill the gonoduct for a distance of about seven body widths. Ovary immature, short, with 11 oocytes in a row. Rectum and anus obscure. Tail end cylindroid, terminus obtuse.

#### **Type species**

*Robleus cylindricus* Massey, 1974 (= sp. inq.) (type designation by monotypy, being the only nominal species in the genus; ICZN Article 68(d))

No other species.

ETYMOLOGY. Patronym honouring Mr Robert Lee Verzino, grandson of the proposer of the name, Dr Calvin L. Massey.

*Robleus cylindricus* was found associated with *Dendroctonus frontalis* in loblolly pine in Texas, USA. As pointed out by Massey (1974), the preadult female of *R. cylindricus* could be the free-living infective stage of an insect parasite (probably the parasite of southern pine beetle). Notwithstanding the good description of the type species, the systematic position of *Robleus* is uncertain. Until other stages of the nematode's life cycle were known, *Robleus* and *R. cylindricus* were proposed by Siddiqi (1986) as genus dubium and species inquirenda, respectively.

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